U.S. Department
of Commerce

Volume 97
Number 3
July 1999

Fishery Bulletin

U.S. Department of Commerce

William M. Daley
Secretary

National Oceanic and Atmospheric Administration

D. James Baker
Under Secretary for Oceans and Atmosphere

National Marine Fisheries Service

Penelope D. Dalton
Assistant Administrator for Fisheries

Fishery Bulletin

Scientific Editor
Dr. John V. Merriner

Kimberly Murray
Editorial Assistant

Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA
101 Pivers Island Road
Beaufort, NC 28516

Managing Editor
Sharyn Matriotti
National Marine Fisheries Service
Scientific Publications Office
7600 Sand Point Way NE, BIN C15700
Seattle, Washington 98115-0070

Editorial Committee
Dr. Andrew E. Dizon National Marine Fisheries Service
Dr. Harlyn O. Halvorson University of Massachusetts, Boston
Dr. Ronald W. Hardy University of Idaho, Hagerman
Dr. Richard D. Methot National Marine Fisheries Service
Dr. Theodore W. Pietsch University of Washington, Seattle
Dr. Joseph E. Powers National Marine Fisheries Service
Dr. Harald Rosenthal Universität Kiel, Germany
Dr. Fredric M. Serchuk National Marine Fisheries Service

The *Fishery Bulletin* (ISSN 0090-0656) is published quarterly by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115-0070. Periodicals postage is paid at Seattle, WA, and at additional mailing offices. POSTMASTER: Send address changes for subscriptions to Fishery Bulletin, Superintendent of Documents, Attn.: Chief, Mail List Branch, Mail Stop SSOM, Washington, DC 20402-9373.

Although the contents of this publication have not been copyrighted and may be reprinted entirely, reference to source is appreciated.

The Secretary of Commerce has determined that the publication of this periodical is necessary according to law for the transaction of public business of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget.

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. Subscription price per year: $43.00 domestic and $53.75 foreign. Cost per single issue: $19.00 domestic and $23.76 foreign. **See back for order form.**

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. It began as the Bulletin of the United States Fish Commission in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

U.S. Department
of Commerce
Seattle, Washington

Volume 97
Number 3
July 1999

Fishery Bulletin

Contents

Articles

411–420 **Austin, Herbert M., Daniel Scoles, and Allison J. Abell**
Morphometric separation of annual cohorts within mid-Atlantic bluefish, *Pomatomus saltatrix*, using discriminant function analysis

421–433 **Bertignac, Michel, John Hampton, and Atilio L. Coan Jr.**
Estimates of exploitation rates for north Pacific albacore, *Thunnus alalunga*, from tagging data

434–448 **Broadhurst, Matt K., Roger B. Larsen, Steven J. Kennelly, and Paul E. McShane**
Use and success of composite square-mesh codends in reducing bycatch and in improving size-selectivity of prawns in Gulf St. Vincent, South Australia

449–458 **DeMartini, Edward E., and Boulderson B. Lau**
Morphometric criteria for estimating sexual maturity in two snappers, *Etelis carbunculus* and *Pristipomoides sieboldii*

459–471 **Franks, James S., James R. Warren, and Michael V. Buchanan**
Age and growth of cobia, *Rachycentron canadum*, from the northeastern Gulf of Mexico

472–481 **Friedland, Kevin D., Jean-Denis Dutil, and Teresa Sadusky**
Growth patterns in postsmolts and the nature of the marine juvenile nursery for Atlantic salmon, *Salmo salar*

482–494 **Hannah, Robert W.**
A new method for indexing spawning stock and recruitment in ocean shrimp, *Pandalus jordani*, and preliminary evidence for a stock-recruitment relationship

495–507 **Labropoulou, Mary, Athanasios Machias, and Nikolaos Tsimenides**
Habitat selection and diet of juvenile red porgy, *Pagrus, pagrus*, (Linnaeus, 1758)

508–525 **Lindeman, Kenyon C., and David B. Snyder**
Nearshore hardbottom fishes of southeast Florida and effects of habitat burial caused by dredging

526–541 **Nates, Sergio F., and Darryl L. Felder**
Growth and maturation of the ghost shrimp *Lepidophthalmus sinuensis* Lemaitre and Rodrigues, 1991 (Crustacea, Decapoda, Callianassidae), a burrowing pest in penaeid shrimp culture ponds

542–554 **Perkins, Peter C., and Elizabeth F. Edwards**
Capture rate as a function of school size in pantropical spotted dolphins, *Stenella attenuata*, in the eastern tropical Pacific Ocean

The National Marine Fisheries Service (NMFS) does not approve, recommend, or endorse any proprietary product or proprietary material mentioned in this publication. No reference shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends, or endorses any proprietary product or proprietary material mentioned herein, or which has as its purpose an intent to cause directly or indirectly the advertised product to be used or purchased because of this NMFS publication.

555–569 **Rilling, Gene C., and Edward D. Houde**
Regional and temporal variability in growth and mortality of bay anchovy, *Anchoa mitchilli*, larvae in Chesapeake Bay

570–580 **Roa, Rubén, Billy Ernst, and Fabián Tapia**
Estimation of size at sexual maturity: an evaluation of analytical and resampling procedures

581–590 **Rooker, Jay R., Scott A. Holt, G. Joan Holt, and Lea A. Fuiman**
Spatial and temporal variability in growth, mortality, and recruitment potential of postsettlement red drum, *Sciaenops ocellatus*, in a subtropical estuary

591–603 **Sigler, Michael F.**
Estimation of sablefish, *Anoplopoma fimbria*, abundance off Alaska with an age-structured population model

604–616 **Sladek Nowlis, Joshua, and Callum M. Roberts**
Fisheries benefits and optimal design of marine reserves

617–625 **Somerton, David A., and Robert S. Otto**
Net efficiency of a survey trawl for snow crab, *Chionoecetes opilio*, and Tanner crab, *C. bairdi*

626–635 **Szedlmayer, Stephen T., and Joseph Conti**
Nursery habitats, growth rates, and seasonality of age-0 red snapper, *Lutjanus campechanus*, in the northeast Gulf of Mexico

636–645 **Thomas, Ross, and Natalie A. Moltschaniwskyj**
Ontogenetic changes in size and shape of statoliths: implications for age and growth of the short-lived tropical squid *Sepioteuthis lessoniana* (Cephalopoda: Loliginidae)

646–660 **Valle, Charles F., John W. O'Brien, and Kris B. Wiese**
Differential hatitat use by California halibut, *Paralichthys californicus*, barred sand bass, *Paralabrax nebulifer*, and other juvenile fishes in Alamitos Bay, California

661–679 **Van Eeckhaute, Lutgarde A. M., Stratis Gavaris, and Edward A. Trippel**
Movements of haddock, *Melanogrammus aeglefinus*, on eastern Georges Bank determined from a population model incorporating temporal and spatial detail

680–689 **Woodbury, David**
Reduction of growth in otoliths of widow and yellowtail rockfish (*Sebastes entomelas* and *S. flavidus*) during the 1983 El Niño

690–701 **Xiao, Yongshun**
General age- and time-dependent growth models for animals

702–712 **Ye, Yimin, and Hussain M. A. Mohammed**
An analysis of variation in catchability of green tiger prawn, *Penaeus semisulcatus*, in waters off Kuwait

Notes

713–716 **Griffith, Jason N., Andrew P. Hendry, and Thomas P. Quinn**
Straying of adult sockeye salmon, *Oncorhynchus nerka*, entering a non-natal hatchery

717–721 **Hunt, Sharon L., Timothy J. Mulligan, and Kenichiro Komori**
Oceanic feeding habits of chinook salmon, *Oncorhynchus tshawytscha*, off northern California

722–729 **Porter, Steven M., and Gail H. Theilacker**
The development of the digestive tract and eye in larval walleye pollock, *Theragra chalcogramma*

730–735 **Winner, Brent L., Robert H. McMichael Jr., and Laurel L. Brant**
Evaluation of small T-anchor and dart tags for use in marking hatchery-reared juvenile red drum, *Sciaenops ocellatus*

736 *Erratum*

737 *Subscription form*

Papers for *Fishery Bulletin 97(3)* were reviewed and accepted for publication under the direction of the previous scientific editor, Dr. John Pearce, and his editorial assistant, Laura Garner.

Morphometric separation of annual cohorts within mid-Atlantic bluefish, *Pomatomus saltatrix*, using discriminant function analysis*

Herbert M. Austin

Daniel Scoles

Allison J. Abell

School of Marine Science
Virginia Institute of Marine Science
College of William and Mary
Gloucester Point, Virginia 23062
E-mail address (for H. M. Austin): Haustin@vims.edu

Abstract.—Larval and tagging studies neither support nor refute the existence of two mid-Atlantic stocks of bluefish, *Pomatomus saltatrix*, one that spawns just south of Hatteras, North Carolina, in the spring, and the other off New England in the summer. Subsequent studies have suggested either a continuous spawning with two survival events, or two distinct spawning events, one in spring south of Hatteras, NC, and a second in mid-summer from Long Island to New England. Genetic studies have supported a single stock because they show the existence of a single gene pool. A stepwise linear discriminant function analysis (DFA) of morphometrics of "spring-spawned" yearling (200–400 mm) and older (>400 mm) bluefish did not classify fish by probable spawning cohort. It did, however separate the yearling fish (200–400 mm) by year class rather than geographic or seasonal spawning. Older fish (>400 mm) showed less separation because multiple (2–10) year classes were present. The DNA studies have revealed genetic homogeneity among these fish. This finding suggests that the morphological characteristics are phenotypically plastic and are influenced each year by the physical environment during spawning and the early juvenile stages.

Manuscript accepted 14 August 1998.
Fish. Bull. 97:411–420 (1999).

The question of bluefish (*Pomatomus saltatrix)* stock composition along the east coast of the United States has been of considerable interest to fisheries scientists for 30 years and has recently (since 1986) become the focus of discussion by management agencies, primarily the Atlantic States Marine Fisheries Commission (ASMFC) and Mid-Atlantic Fisheries Management Council (MAFMC) (Anonymous, 1989). The problems of managing fisheries when the stock composition and boundaries are unclear have hampered effective management of weakfish, *Cynoscion regalis*, summer flounder, *Paralichthys dentatus*, surf clam, *Spisula solidissima*, and striped bass, *Morone saxatilis* by the ASMFC or MAFMC (or both) because current management practices manage by unit (genetic) stock. Interstate management is further hampered when a unit stock exhibits differential spatial reproduction and migration patterns (e.g. weakfish, Scoles, 1990).

The stock structure of the bluefish (*Pomatomus saltatrix*) in the western mid-Atlantic region is not well understood. Lund (1961) recorded meristic counts of gill rakers along the first branchial arch of young fish and suggested that six separate stocks of bluefish occur along the western north Atlantic coast of the United States. He later suggested the occurrence of several races in this region on the basis of results of two mark-recapture studies (Beaumariage and Wittich, 1966; Lund and Maltezos, 1970). These results were not supportive of Lund's original six stock concept because they suggested that there might be a "Florida" or "South Atlantic Bight" and a "northern" or "mid-Atlantic Bight" stock. Subsequent analyses of temporal and spatial distributions of bluefish in the ichthyoplankton, and spawning times, suggested two north Atlantic stocks (Norcross et al, 1974; Kendall and Walford, 1979), in addition to a south Atlantic or Florida Stock (Collins and Stender, 1987).

Chiarella and Conover (1990), on the other hand, using back calculations of scales, demonstrated that most spawning in the north mid-Atlantic Bight (MAB) occurs during mid-summer (July) and is composed of spring-spawned fish, both of which suggest a single stock. They also found from back calculations that most yearling fish (260 mm) collected in waters along Long

* Contribution 2143 from the Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA.

Island during 1986–87 were spring-spawned. Later, McBride and Conover (1991), looking at young-of-the-year bluefish in the New York Bight during the summers of 1987 and 1988, found two discrete size groups by late summer (150 mm, 75 mm). Their otolith analyses confirmed that the fish represented both spring- and summer-spawned cohorts.

More recent larval studies (Smith et al., 1994; Hare and Cowen, 1993) suggest an alternate hypothesis, that of a continuous wave of spawning by a single stock from off Hatteras in April–May to off Cape Cod or Block Island in June–July with two survival events, one in spring and one later in the summer as a result of oceanographic conditions. These survival events may have led to the previous hypothesis of two distinct spawning events. At any rate, the genetic analyses of Graves et al. (1993), using mtDNA, have shown that progeny from both the spring and summer spawning were of the same stock, and that mid-Atlantic Bight bluefish compose a single genetic stock. The various hypotheses have been revisited by Juanes et al. (1996) in a review of global bluefish early life history.

A characterization of the seasonal movement and spawning of what was then (1977) considered the north Atlantic stocks was summarized by Wilk (1977). Before the advent of routine genetic testing, Wilk (1977) conducted a morphometric analysis of yearling fish from the North Carolina sounds and Middle Atlantic Bight to test the hypothesis that two stocks of bluefish occurred in the mid-Atlantic Bight. The preliminary data, results, and manuscript were lost in the 1984 NMFS/NOAA Sandy Hook Marine Laboratory fire. Wilk did find morphometric differences that were statistically significant (Wilk[1]). If these two geographically separate spawnings are by the same stock, as demonstrated by Graves et al. (1993), but exhibit morphological differences as suggested by Wilk, perhaps due to environmental phenotypic plasticity, then a potentially valuable tool for management exists, particularly if growth, and recruitment or harvest pressure (or both) are different. With this possibility in mind, we conducted a morphometric analysis of bluefish collected in the mid-Atlantic Bight of the U.S. east coast.

Methods

A total of 1386 bluefish, ranging in size from 93 to 888 mm TL, were collected from April 1987 through April 1990 from several locations between eastern Long Island, New York, and Beaufort, North Carolina. Samples were pooled on the basis of geography and date-year of collection (Tables 1 and 2). Most were collected from pound and gill nets, but several small fish were taken by 10.8-m (30-ft) otter trawl. The majority of fish over 600 mm TL were collected by hook and line tournament fishermen.

Twenty two morphometric measurements were recorded from the left side of the fish with a meter stick or dial calipers to the nearest millimeter. Names of morphometric variables and abbreviations are provided in Table 3. Scales were removed from under the pectoral fin of each fish, mounted on acetate sheets, and ages were determined with a microfilm reader according to the techniques of Hill and Loesch.[2]

Samples were classified by using stepwise linear discriminant function analysis (DFA) (Fisher, 1936) with SPSS software program (Norusis, 1985). An excellent introduction to the statistics of discriminant analysis is presented by Klecka (1989) in which all assumptions and shortcomings of the methods are discussed. Allometric growth can cause bias, and although it is recognized that it is impossible to remove all allometric bias, Riest (1985), in a review of transformation methods, has offered Thorpe's (1975) as among the best in this situation. Schaefer (1990) and Scoles (1990) also used this technique and found it satisfactory for removing size effects during morphometric analyses of tuna and weakfish.

Consequently, all measurements were transformed following equations taken from Thorpe (1975) where

$$\hat{\hat{Y}}_i = 10^{\hat{Y}}$$

$$\hat{Y}_i = \log_{10} Y_i - b(\log_{10} X_i - \log_{10} \bar{\bar{X}})$$

where $\hat{\hat{Y}}_i$ = the adjusted variable of the ith specimen;
Y_i = the variable to be transformed of the ith specimen;
b = the allometric coefficient;
X_i = a standard measure of size of the ith specimen for which fork length was used; and
$\bar{\bar{X}}$ = the grand mean of standard lengths.

A third equation, combining the first two provides

$$\mathrm{Log}_{10}\left[Y_i / \hat{\hat{Y}}_i\right] = b\mathrm{Log}_{10}\left[X_i / \bar{\bar{X}}_i\right],$$

[1] Wilk, S. 1989. Sandy Hook Marine Laboratory, National Marine Fisheries Service, NOAA, Sandy Hook, NJ. Personal commun.

[2] Hill, B., and J. Loesch. 1989. Striped bass research in Virginia: characterization of Virginia commercial fisheries. Annual Report 88-89, 22 p. Virginia Institute of Marine Science, P.O. 1346, Gloucester Point, VA 23062.

Table 1

Bluefish collection data: date, location, number of fish collected, and gear used in collection. L.I.= Long Island; L.I.S. = Long Island Sound.

Date	Location	*n*	Gear
10 Mar 1987	Hatteras, NC	8	Gill net
30 Apr 1987	Aberdeen Creek, VA	10	Gill net
30 Apr 1987	Mobjack Bay, VA	21	Gill net
17 May 1987	Chesapeake Bay, VA	32	Hook and line
14 Jul 1987	Hatteras, NC	16	Seine
8 Jul 1987	Mobjack, VA	12	Gill net
2 Oct 1987	New Jersey	11	Trawl
6 Nov 1987	Chesapeake Bay, V	44	Hook and line
12 Apr 1988	Norfolk, VA	20	Gill Net
19 Apr 1988	Rappahannock R.	19	Pound net
1 May 1988	York River, VA	10	Pound net
12 May 1988	York River, VA	1	Pound net
16 Jun 1988	Ches. Bay, VA	58	Hook and line
18 Jul 1988	Pt. Lookout, L.I.	50	Gill net
19 Jul 1988	Peconic Bay, L.I.	24	Gill net
19 Jul 1988	Montauk, L.I.	71	Hook and line
25 Jul 1988	York River, VA	26	Pound net
28 Jul 1988	Hatteras, NC	85	Pound net
3 Aug 1988	York River, VA	8	Pound net
5 Aug 1988	York River, VA	76	Pound net
5 Aug 1988	L.I.S., CT	15	Trawl
9 Sep 1988	L.I.S., CT	171	Trawl
9 Sep. 1988	Potomac R.	69	Hook and line
4 Apr 1989	Pamlico Sound	81	Various
4 Apr 1989	Oregon Inlet, NC	169	Various
15 June 1989	Reedville, VA	86	Hook and line
25 July 1989	New York, NY	51	Various
15 Aug 1989	York River, VA	103	Pound net
9 Sep 1989	Hatteras, NC	42	Pound net

which more clearly shows Y_i is an estimate of the average Y_i for an individual of fork length X_i.

Following transformation, each variable was regressed against fork length (FL). The slope of each transformed variable on FL was zero or insignificant in all cases; therefore effects of allometry were disregarded. The results were plotted for visual inspection of outliers which were removed before subsequent analyses if they were outside the range of biological possibility, and thus suggested measurement error. Consequently, two subgroups of data were developed. The first included bluefish between 200 and 400 mm fork length (yearlings), to remove young-of-the-year from the data which are in the stage of growth most likely to show allometry and to duplicate the size range used by Wilk and Walford in 1964 (Wilk, 1977). The second group included bluefish greater than 400 mm fork length.

The linear discriminant function used here is of the form

$$D = B_1X_1 + B_2X_2 + B_3X_3 + \ldots\ldots\ldots B_nX_n + C$$

and is similar to a multiple linear regression

where D = the discriminant function that characterizes each reference group;
X_n's = the independent variables (individual measurements) selected at in a stepwise fashion; and

Table 2

Discriminant function analysis sample groupings by location, year, and size category. Ches Bay = Chesapeake Bay.

Group	Year	ID number	Sample size and length range (mm, in parentheses) 200–400 mm	>400 mm
Summer Hatteras	1987	1	14 (303–382)	2 (417–441)
Summer Ches Bay	1987	2	10 (258–316)	37 (448–884)
Spring Hatteras	1987	3	—	8 (684–765)
Spring Ches Bay	1987	4	15 (325–385)	30 (801–852)
Summer Ches Bay	1988	5	11 (225–382)	106 (570–830)
Summer Long Isl.	1988	6	7 (219–395)	174 (555–811)
Spring VA Coast	1988	7	—	13 (471–731)
Spring Ches Bay	1988	8	—	26 (471–757)
Summer Ches Bay	1988	9	104 (245–291)	—
Summer Hatteras	1988	10	85 (235–321)	—
Spring Hatteras	1989	11	42 (357–398)	101 (477–784)
Summer Ches Bay	1989	12	128 (215–352)	51 (405–525)
Summer Long Isl.	1989	13	—	44 (418–734)
Summer Hatteras	1989	14	—	29 (412–516)
Spring Pamlico	1989	15	71 (357–398)	7 (402–715)
Spring Ches Bay	1990	16	26[1]	30[1]
			524 (215–398)	658 (402–884)

[1] Length data lost.

Table 3

List of morphometric measurements on bluefish. Abbreviations and name of variable are those used in text.

Abbreviation	Description
PMX	Premaxilla
MAX	Maxilla
IOB	Interorbital
POB	Postorbital
POP	Preoperculum ("cheek")
OPC	Operculum
HDP	Head depth
PCO	Pectoral fin origin
PCI	Pectoral fin insertion
PLO	Pelvic fin origin
PLI	Pelvic fin insertion
VNT	Vent
AFO	Anal fin origin
AFI	Anal fin insertion
D1O	First dorsal fin origin
D1I	First dorsal fin insertion
D2O	Second dorsal fin origin
D2I	Second dorsal fin insertion
GTH	Girth
TOL	Total length
FKL	Fork length
STL	Standard length
DSP	First and second dorsal space

B_n's = the coefficients or "unstandardized function coefficients"; and
C = a constant.

Initially we intended to follow the 1960s methods of Wilk (1977) by assigning a spring-southern and summer-northern *a priori* reference designation. We were unable however, to collect a reference group of spring- and summer-spawned yearling bluefish. From the length frequencies of the yearling fish (211–382 mm) that we collected, it appeared that all were "spring-spawned" (Chiarella and Conover, 1990). As a result we made no effort *a priori* to separate "spring- spawned" from "summer-spawned" yearling fish on the basis of scale back calculations as Chiarella and Conover (1990) had done but assumed all were spring-spawned. *A priori* assignment of reference or learning groups is often used to determine the discriminant function which is then used to classify the individuals of known origin to one or the other reference groups. If, however, more than two stocks are present, the individuals of the third stock will be "force fitted" into one of the reference groups. Rather than forcing *a priori* assignments of two groups, and to identify possible additional stocks (from the south [McBride et al. 1993]) or morphometrically distinct

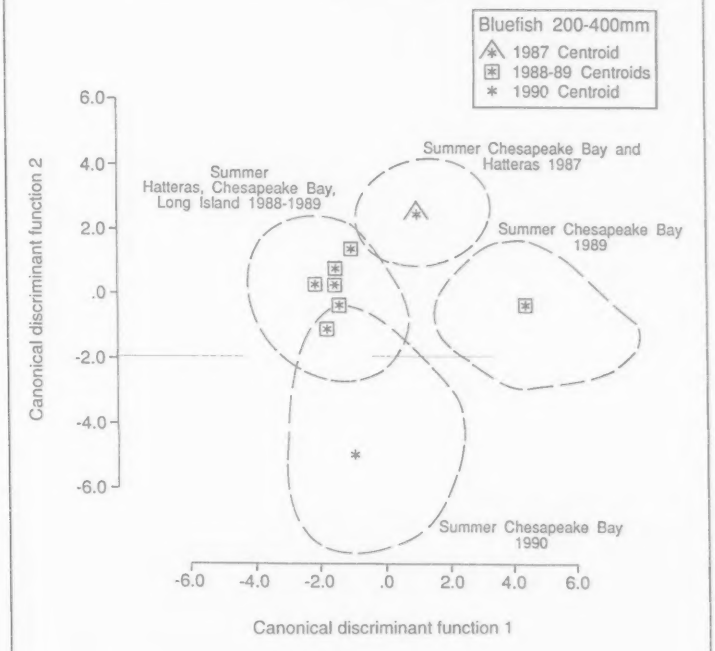


Figure 1

Scatterplot of canonical discriminant functions 1 and 2 for bluefish 200–400 mm showing locations of group centroids for 1987–90 by geographic area of collection.

groups as Wilk (1977) found, we conducted the DFA without *a priori* assignments.

Finally, an unweighted paired group method (UPGM) of clustering with arithmetic averages, a form of cluster analysis, was run to examine the relative distance between group centroids. Centroids that appear in a cluster are morphologically similar.

Results

The first five canonical functions are listed because they carry the analysis through the 95% cumulative percentage for fish 200–400 mm (Tables 4 and 5); seven functions are included for the fish >400 mm; however, the eigenvalues (Tables 5 and 6) show that only the first two functions are important in each case. The discriminant scores and centroids from functions 1 and 2 were plotted against each other to develop a graphic representation of the relationship among groups (Figs. 1 and 2).

Wilk's 1960's (1977) analysis found that the inter-dorsal space was a discriminating character. To provide a comparison, we computed an "inter-dorsal

Table 4

Summary of stepwise discriminant function analysis for 16 groups and 16 morphometric characters. Fish were 200–400 mm FL. See Table 3 for definitions of variables.

Step no.	Variable entered	Wilk's lambda	Minimum *P*	*D*	*P*
1	PLI	0.44335	<0.0001	0.00764	0.8081
2	HDP	0.34477	<0.0001	0.23817	0.2317
3	MAX	0.25160	<0.0001	0.65660	<0.0001
4	DSP	0.16585	<0.0001	0.87455	0.0001
5	IOB	0.13113	<0.0001	1.20062	<0.0001
6	OPC	0.12388	<0.0001	1.29810	<0.0001
7	PCO	0.10184	<0.0001	1.44335	<0.0001
8	AFO	0.09450	<0.0001	1.47319	<0.0001
9	D2I	0.08292	<0.0001	1.55493	<0.0001
10	D1O	0.07776	<0.0001	1.62040	<0.0001
11	AFI	0.07325	<0.0001	1.67691	<0.0001
12	POB	0.06806	<0.0001	1.69120	<0.0001
13	POP	0.06544	<0.0001	1.70979	<0.0001
14	PMX	0.05928	<0.0001	1.72065	<0.0001
15	PLO	0.05329	<0.0001	1.72103	0.0001
16	D1I	0.04386	<0.0001	1.72130	0.0001

Table 5

Summary of first five canonical discriminant functions. Fish were 200–400 mm FL.

Function	Eigenvalue	Cumulative percent	Canonical correlation	Wilk's lambda	Chi squared	df	*P*
1	2.29051	48.91	0.834324	0.15912	935.6	150	<0.0001
2	1.16710	73.84	0.733863	0.34483	541.6	126	<0.0001
3	0.54375	85.45	0.593486	0.53234	320.9	104	<0.0001
4	0.28451	91.53	0.470633	0.68379	193.5	84	<0.0001
5	0.14586	94.64	0.356785	0.78354	124.2	66	<0.0001

Table 6

Summary of the first seven canonical discriminant functions. Fish were >400 mm FL.

Function	Eigenvalue	Cumulative percent	Canonical correlation	Wilk's lambda	Chi squared	df	*P*
1	1.4858	42.4	0.77312	0.1880	1072.9	180	<0.0001
2	0.8153	65.6	0.67016	0.3413	690.1	154	<0.0001
3	0.4462	78.4	0.55546	0.4936	453.2	130	<0.0001
4	0.2595	85.8	0.45387	0.6217	305.1	108	<0.0001
5	0.1682	90.6	0.37945	0.7263	205.3	88	<0.0001
6	0.0900	93.1	0.27740	0.7917	149.9	70	<0.0001
7	0.0769	95.4	0.26722	0.8526	102.4	54	<0.0001

Table 7

Summary of stepwise discriminant function analysis for 16 groups and 16 morphometric characters. Fish were >400 mm FL. See Table 3 for definitions of variables.

Step no.	Variable entered	Wilk's lambda	Minimum *P*	Minimum *D*	Minimum *P*
1	D1I	0.7177	<0.0001	0.0007	0.9364
2	POP	0.6367	<0.0001	0.0288	0.8088
3	PLO	0.4628	<0.0001	0.2543	0.0520
4	DSP	0.4326	<0.0001	0.4455	0.1638
5	HDP	0.2946	<0.0001	0.6365	0.0008
6	AFO	0.2645	<0.0001	0.7851	0.0237
7	PCO	0.2483	<0.0001	0.8786	0.0225
8	PLI	0.1813	<0.0001	1.0243	<0.0001
9	D1O	0.1653	<0.0001	1.2288	<0.0001
10	POB	0.1323	<0.0001	1.2774	<0.0001
11	IOB	0.1090	<0.0001	1.3481	<0.0001
12	D2I	0.1025	<0.0001	1.4211	<0.0001
13	OPC	0.0994	<0.0001	1.4769	<0.0001
14	MAX	0.0996	<0.0001	1.5093	<0.0001
15	PMX	0.0776	<0.0001	1.5274	<0.0001
16	AFI	0.0756	<0.0001	1.5402	<0.0001

space" term (DSP), as the difference between the first dorsal insertion (D1I) less the second dorsal origin (D2O). When the analysis was run with this new variable (DSP), it was selected as an important term in the functions (Tables 4 and 9).

The centroids for yearling fish do not fall into two classes, which would have suggested either a geographic north-south or temporal spring-summer spawned classification (Fig. 1); rather they fall into three clusters of cohorts by year class, regardless of geography of collection site (Table 10). For example, collections during 1987 at Hatteras, North Carolina, and Chesapeake Bay, Virginia (the 1986 year class), are separate and distinct from both the 1988 and 1989 collections (1987 and 1988 year classes) and also from the Hatteras and Chesapeake Bay collections. Further, the 1989 collections (1988 year class) were classified into two groups, one of which was the same as the 1988 collection. The 1990 collection (1989 year class) fell in between 1988 and 1989, overlapping both.

The centroids of the large fish (>400 mm), a mixture of up to 10 year classes in a sample, showed little geographic, temporal, or year-class classification (Fig. 2).

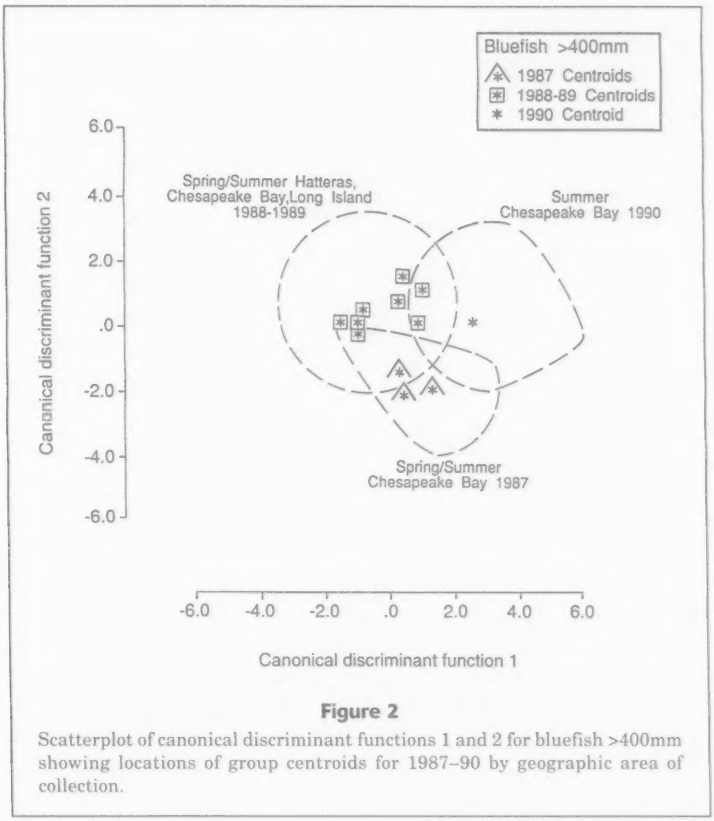


Figure 2

Scatterplot of canonical discriminant functions 1 and 2 for bluefish >400mm showing locations of group centroids for 1987–90 by geographic area of collection.

Discussion

Several authors (Nyman and Conover, 1988; McBride, 1989; Simpson et al., 1990) working in the Long Island region and analyzing length-frequency data, reported exclusively spring-spawned young-of-the-year during 1985–86. Both spring-spawned and some late arriving summer-spawned young-of-the-year were collected there in 1987, and then a shift occurred to predominantly summer-spawned fish during the summer-fall of 1988.

Because ratios continued to be similar for the yearling fish in our collections and because length frequencies were also similar, our 1987 samples from Hatteras and the Chesapeake Bay were apparently from the predominantly spring-spawned 1986 year class. Our 1988 samples, the 1987 year class, were also predominantly spring spawned but were classified morphologically separate from the 1986 year class.

Our 1989 samples (the 1988 year class) from Hatteras, Chesapeake Bay, and Long Island showed a split classification, some the same as our 1988 samples (the 1987 year class) and the rest, separate from both 1987 and 1988 year classes. The 1990 samples, from a dominant 1989 year class, collected in the Chesapeake Bay, overlapped slightly between the 1987 and 1988 year classes (Fig. 1).

If the shift from spring-spawned to summer-spawned young-of-the-year noted by the above authors for Long Island holds for Chesapeake-Hatteras yearling fish, then the morphologically distinct 1986 year class from our 1987 collections was composed of spring-spawned fish. The 1988–90 collections of the 1987–89 year classes, may be a mix of spring- and summer-spawned fish but show no separation. As stated earlier, however, our length frequencies of yearling fish in all years (1987–90) suggest that our samples were all spring-spawned fish (Table 2). An alternate explanation is that the morphologically distinct yearling fish, representing separate year classes or annual cohorts, and spawned in differing environments each year are demonstrating environmental or phenotypic plasticity. That is, that their morphological characters are environmentally determined and are different each year.

Table 8

Canonical discriminant function coefficients linear discriminant equation (Norusis, 1985): $D = B_0 + B_1X_1 + B_2X_2 + B_3X_3 \ldots\ldots B_nX_n$. See Table 3 for definitions of variables.

	Unstandardized function coefficients			
	200-400 mm FL function		>400 mm FL function	
Variable	1	2	1	2
PMX	−11.3805	−7.5218	−5.8925	−27.9831
MAX	1.2972	4.1059	8.0311	30.1133
IOB	11.3277	−0.4940	2.0227	24.8566
POB	−6.1778	−18.1707	−5.7929	−45.9063
POP	6.1848	4.7921	−5.1122	25.7729
OPC	−26.3362	6.4774	−2.5250	−29.3489
HDP	−0.6669	29.7938	26.4669	17.4505
PCO	36.7537	−2.9036	1.8195	−20.8899
PLO	10.1294	−13.7243	20.1050	−4.4471
PLI	26.8615	31.4590	−57.1219	26.6134
AFO	−31.2089	8.5720	42.9709	−2.0460
AFI	31.6723	35.3519	−24.5871	12.8353
D1O	4.0019	−3.4074	−35.3567	−8.2396
D1I	12.8394	−22.4628	48.7193	−14.1872
DSP	0.2674	3.7165	1.3185	1.3386
D2I	32.9298	−6.5686	3.9964	39.1365
CONSTANT	−212.7263	−118.6822	−45.9465	−78.7146

Table 9

Canonical discriminant function group centroid means. * = no collections from this size group

	200–400 mm		>400 mm	
Group	Function 1	Function 2	Function 1	Function 2
1	−1.1747	−2.4628	2.2954	−4.1523
2	−1.8353	−4.8299	−0.7644	−2.2536
3	*		−0.9446	0.5734
4	−1.4581	−2.4707	−0.4563	−2.1051
5	0.2588	1.6696	0.9954	0.6740
6	−0.4975	0.3665	1.3013	−0.0488
7	*		0.8351	−0.6780
8	*		1.4361	−0.1726
9	−1.4280	−0.0648	*	
10	−1.0596	0.8962	*	
11	−0.7187	1.0913	−0.0650	0.3479
12	2.2186	−0.3778	−1.1776	0.1391
13	*		−1.5116	0.4816
14	2.7864	1.0578	−1.3068	1.6483
15	−0.2675	0.3093	−0.7993	0.5799
16	1.1706	−0.0615	−1.9122	0.4894

The larger fish in this study are a composite of at least ten year classes (2–11 years); therefore separation or classification would be expected to be less precise. Indeed there was considerable overlap in classification of the larger fish (Table 10).

From results of the DFA, and in light of the back calculations of Chiarella and Conover (1990) and the genetic data of Graves et al. (1993), it would appear that there is only one stock of bluefish in the mid-Atlantic Bight and that the morphometric differences among bluefish cohorts are a result of phenotypic plasticity. Because the environment at the time of spawning and juvenile development varies geographically and interannually, so too will morphometric features. As the fish grow, their plastic morphological characters, expressed as an index of character length versus fish length, become less and less reliable; when year classes mix, as in our >400 mm sample, they provide no discriminant characterization unless separated by individual year class.

Although a single genetic stock, the two MAB cohorts (spring- and summer-spawned), may exhibit interannual differential recruitment success and survival to yearlings. In addition, the reported differences in growth, seasons and location of spawning, migration routes, and variations in fishing mortality along the MAB can complicate management efforts if the two cohorts are managed as a single stock. Even for a single mid-Atlantic genetic stock, recruitment variations between spring and summer cohorts may be significant, year to year, and consideration should be given to monitoring the annual contribution of the spring-spawned and summer-spawned cohorts as the stock may be healthier when the spring-spawned predominate for several years running (Chiarella and Conover, 1990). The morphometric separation by year class provides evidence that the environment likely affects bluefish size and shape; this may prove to be a useful tool in separating yearling bluefish by the geographic area in which they spent their first year of development.

Conclusions

Previous larval and tagging studies neither support nor refute the existence of one or more MAB bluefish stocks, one that spawns just south of Hatteras, North Carolina, in the spring and the other off New England in the summer. The mtDNA analysis by Graves et al. (1993) suggests that there is one mid-Atlantic stock which from our results produces several environmentally induced morphotypes.

Table 10

Classification results by geographic area and year for fish 200–400 mm FL and fish >400 mm FL. SU = Summer; SP = Spring; HA = Hatteras; CB = Chesapeake Bay; LI = Long Island; PS = Pamlico Sound, NC.

Group	Group number	Predicted group membership (%)																
		n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
200–400 mm FL																		
SU/HA/87	1	14	64	7							7			7			14	
SU/CB/87	2	10		100														
SP/CB/87	4	15	7			47					27	13					7	
SU/CB/88	5	11					46					27					9	18
SU/LI/88	6	7				29	14				29		14					14
SU/CB/88	9	104	1				1				76	14	3				3	2
SU/HA/88	10	85				1					19	61	7	1			11	
SP/HA/89	11	42									2	36	55	2			5	
SU/CB/89	12	128				1					5	2	2	79		2	3	6
SU/HA/89	14	11												64		27	9	
SP/PS/89	15	71									13	16	1	1			69	
SU/CB/90	16	26	4								4	4	15				4	69
>400 mm FL																		
SU/HA/87	1	2	100															
SU/CB/87	2	37		73		14		8						3				3
SP/HA/87	3	8			88								12					
SP/CB/87	4	30		13		70	7	7		3								
SU/CB/88	5	106				1	53	26		2			9	4		1	1	3
SU/LI/88	6	174		1			8	76	1	1			12	1	1	1		
SU/VC/88	7	13						54	39					7				
SP/CB/88	8	26		4		4	8	27	8	35			15					
SP/HA/89	11	101		2			2	5	1	3			66	7	6	5		4
SP/CB/89	12	51		2		4	4	6	2				33	35	6	6	2	
SU/LI/89	13	44		2	2	2							41	5	41	5		2
SU/HA/89	14	29					10						10		4	69		7
SU/PS/89	15	7												14			86	
SU/CB/90	16	30		7				3					11	12	7	7		47

Acknowledgments

We wish to acknowledge the field assistance of Ana Beardsley and Jan McDowell, as well as the officials of the various Virginia bluefish tournaments that made samples available to us. Critical review was provided by John Graves and Jack Musick of VIMS. The most helpful comments of an anonymous reviewer strengthened the manuscript and we are most grateful to this anonymous colleague. The work was supported by a grant to the Virginia Institute of Marine Science from the U. S. Fish and Wildlife Service, through the Virginia Marine Resources Commission, grant n number F-60-R.

Literature cited

Anonymous.
1989. Bluefish Fisheries Management Plan, Atlantic States Marine Fisheries Commission, Wash., D.C., 54 p.

Beaumariage, D., and A. Wittich.
1966. Returns from the 1964 Schlitz tagging program, Florida. Board Cons. Tech. Ser. 47, 50 p. Florida Dep. Natural Resources, St. Petersburg, FL.

Chiarella, L. A., and D. O. Conover.
1990. Spawning season and first-year growth of adult bluefish from the New York Bight. Trans. Am. Fish. Soc. 119:455–462.

Collins, M. R. and B. W. Stender.
1988. Larval king mackerel (*Scomberomorus cavalla*), Spanish mackerel (*S. maculatus*), and bluefish (*Pomatomus*

saltatrix) off the southeast coast of the United States, 1973–1980. Bull. Mar. Sci., 41:822–834.

Fisher, R.
1936. The use of multiple measurements in taxonomic problems. Ann.-Eugenics 7:179–188.

Graves, J. E., J. R. McDowell, A. M. Beardsley, and D. R. Scoles.
1993. Population genetic structure of the bluefish, *Pomatomus saltatrix*, in Atlantic coastal waters. Fish. Bull. 90:469–475.

Hare, J. A., and R. K. Cowen.
1993. Ecological and evolutionary implications of the larval transport and reproductive strategy of bluefish, *Pomatomus saltatrix*. Mar. Ecol. Prog. Ser. 98:1–16.

Juanes, F., J. A. Hare, and A. G. Miskiewicz.
1996. Comparing early life history strategies of *Pomatomus saltatrix*: a global approach. Mar. Freshwater Res. 47:365–379.

Kendall, A., and L. Walford.
1979. Sources and distribution of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the east coast of the United States. Fish. Bull. 77(1):213–227.

Klecka, W. R.
1989. Discriminant analysis. Series: Quantitative applications in the social sciences. Sage Publ., Inc., Thousand Oaks, CA, 70 p.

Lund, W.
1961. A racial investigation of bluefish, *Pomatomus saltatrix* of the Atlantic Coast of North America. Bol. del Inst'o. Oceanog. Venezuela 1(1):73–129.

Lund, W, and G. Maltezos.
1970. Movements and migrations of the bluefish, *Pomatomus saltatrix* tagged in waters of New York and southern New England. Trans. Am. Fish. Soc., 99(4):719–725.

McBride, R. S.
1989. Comparative growth and abundance of spring- versus summer- spawned young-of-the-year bluefish, *Pomatomus saltatrix*, recruiting to the New York Bight. M.S. thesis submitted to the State Univ. of New York at Stony Brook, NY, 56 p.

McBride, R. S., and D. O. Conover.
1990. Recruitment of young-of-the-year bluefish *Pomatomus saltatrix* to the New York Bight: variation in abundance and growth of spring- and summer-spawned cohorts. Mar. Ecol. Prog. Ser. 78:205–216.

McBride, R. S., J. L. Ross, and D. O. Conover.
1993. Recruitment of bluefish *Pomatomus saltatrix* to estuaries of the U.S. South Atlantic Bight. Fish. Bull. 91:389–395.

Norcross, J. J., S. L. Richardson, W. Massman, and E. Joseph.
1974. Development of young bluefish, *Pomatomus saltatrix* and distribution of eggs and young in Virginia waters. Trans. Am. Fish. Soc. 103(3):477–497.

Norusis, M.
1985. SPSS advanced users guide. SPSS Inc., Chicago, IL, 474 p.

Nyman, R. M., and D. O. Conover.
1988. The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York. Fish. Bull. 86(2):237–250.

Riest, J. D.
1985. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. Can. J. Zool. 63:1429–1439.

Schaefer, K. M.
1990. Geographic variation in morphometric characters and gill-raker counts of yellowfin tuna, *Thunnus albacares*, from the Pacific Ocean. Fish. Bull. 89:289–297.

Scoles, D. R.
1990. Stock identification of weakfish, *Cynoscion regalis*, by discriminant function analysis of morphometric characteristics. M.S. thesis submitted to the College of William and Mary, School of Marine Science, Virginia Institute of Marine Science, Gloucester Point, VA 23062, 51 p.

Simpson, D. G., P. T. Howell, and M. W. Johnson.
1990. Assessment of bluefish in Long Island Sound with reference to the coastwide stock. Section 2, job 6 *in* A study of marine recreational fisheries in Connecticut., p 83–104. Connecticut Dep. Environ. Cons., Hartford, CT.

Smith, W., P. Berrien, and T. Pottoff.
1994. Spawning patterns of bluefish, *Pomatomus saltatrix*, in the northeast continental shelf ecosystem. Bull. Mar. Sci. 54(1):8–16.

Thorpe, R. S.
1975. Quantitative handling of characters useful in snake systematics with particular reference to intraspecific variation in the ringed snake, *Natrix natrix*. Biol. J. Linn. Soc. 7:27–43.

Wilk, S.
1977. Biological and fisheries data on bluefish, *Pomatomus saltatrix*. U.S. Dep. Commer., NMFS/NOAA, Tech. Ser. Rep. 11, 55 p.

Estimates of exploitation rates for north Pacific albacore, *Thunnus alalunga*, from tagging data

Michel Bertignac

John Hampton

Secretariat of the Pacific Community
B.P. D5
98848 Noumea Cedex, New Caledonia
Email address (for M. Bertignac): michelbe@spc.org.nc

Atilio L. Coan Jr.

Southwest Fisheries Science Center
P.O. Box 271
La Jolla, California 92038

Abstract.—North Pacific albacore tagging data from a tag-release program conducted from 1971 to 1989 were analyzed to obtain estimates of exploitation rates and related parameters. The major albacore fishing fleets in the North Pacific, the U.S. baitboat, Japan baitboat, troll and longline fleets were used in the analysis. Another category of fleet ("other") that combined remaining miscellaneous recapture sources was also used. Tag-attrition models incorporating variable availability of tagged albacore to the various fleets, seasonal catchability, and multiyear effects on catchability were developed and applied. The incorporation of all three effects was found to improve model fit significantly. If exploitation of the tagged population is representative of the North Pacific albacore population as a whole and if tag reporting rates were high, the results would suggest that the exploitation rate has been less than 10% per year since the early 1970s. However, a deficit of returns from the troll fleet in comparison with its catch suggested that the pattern of exploitation of the tagged population, by this fleet at least, was different from that for the untagged albacore population. After compensating for assumed depressed availability of tagged albacore to the troll fleet, annual exploitation rates were estimated to have declined from a high of 40% in the mid-1970s to <10% since the early 1980s.

Manuscript accepted 17 August 1998.
Fish. Bull. 97:421–433 (1999).

Albacore tuna, *Thunnus alalunga*, occur in the tropical and subtropical waters of the Pacific Ocean, where they comprise separate stocks north and south of the equator (Murray, 1994). In the north Pacific, albacore spawn predominantly in the spring and summer over a wide area bounded approximately by 10°–30°N (Nishikawa et al., 1985). Juvenile albacore appear in the North Pacific Transition Zone (35°–45°N), where they are exploited by the surface fishery, comprising mainly Japanese and U.S. baitboat, troll, and until the early 1990s, Japanese and Taiwanese driftnet fleets (Fig. 1). Adult albacore are found at lower latitudes, where they are caught by the subsurface longline fishery, comprising Japanese, Korean, and Taiwanese fleets (Fig. 1). Longline catches have been fairly stable at 10,000–20,000 t annually. Total surface fishery catches (which have been dominated by Japanese baitboat catches) have declined from a peak of around 100,000 t in the mid-1970s to 20,000–50,000 t in recent years (Liu and Bartoo, 1995).

Since 1971, 23,780 albacore have been tagged in the North Pacific in a program conducted jointly by the U.S. National Marine Fisheries Service (NMFS) and the American Fishermen's Research Foundation. The tag recoveries have been used in studies of albacore movements (Laurs and Lynn, 1977), growth (Laurs and Wetherall, 1981), and fishery interaction (Kleiber and Baker, 1987). However, to date no formal analysis of the data has been undertaken to estimate exploitation rates and related parameters. In this paper, we develop tag-attrition models (Kleiber et al., 1987), incorporating different structural assumptions concerning availability and catchability of the tagged population. The models are fitted to the albacore tagging data to obtain estimates of the instantaneous rate of natural mortality and fleet-specific catchability coefficients. These estimates are used to construct time series of estimated exploitation rates. The relative merits of the alternative models and applicability of the estimates to the North Pacific albacore population in general are discussed.

Materials and methods

Tagging data

Albacore tagging occurred from 1971 to 1996, mainly during April–Sep-

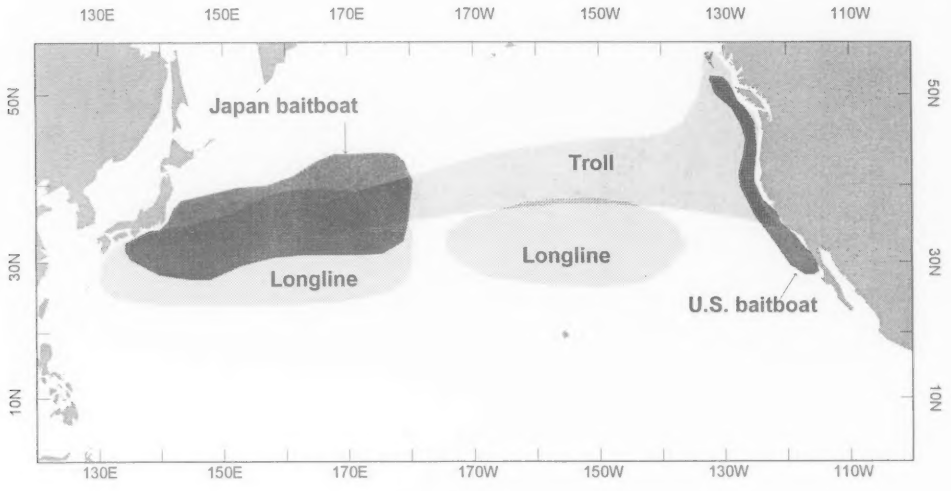


Figure 1
Schematic diagram of geographic distributions of major North Pacific albacore fishing fleets.

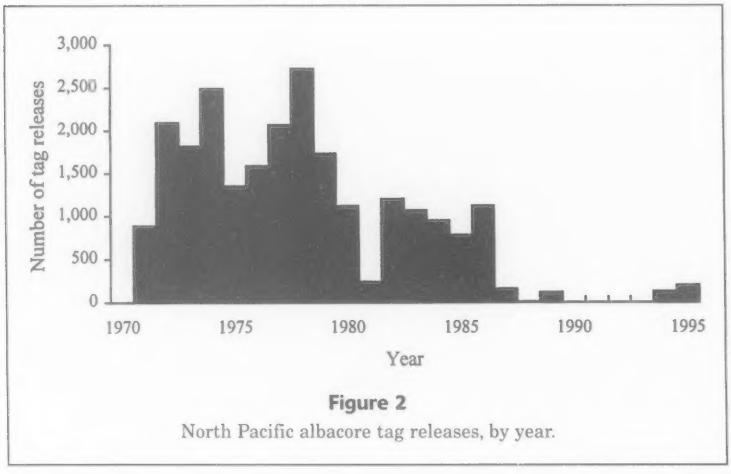


Figure 2
North Pacific albacore tag releases, by year.

tember, with 97% of the 23,780 releases occurring prior to 1987 (Fig. 2). Tagging was carried out aboard U.S. troll vessels and baitboats by NMFS technicians and commercial fishermen trained in tagging. Tagging methods are described by Laurs et al. (1976) and Laurs and Wetherall (1981). Only albacore judged to be in very good condition were selected for tagging; therefore mortality due to tagging is believed to have been negligible. Tagged albacore were released over a wide area of the eastern and central North Pacific; the largest numbers of releases took place in coastal waters adjacent to North America at 30°–50°N (Fig. 3). Fewer albacore were tagged west of 180°, which is the main operational area of the Japanese baitboat fleet. The size distribution of tagged albacore is typical of surface fishery catches (Fig. 4).

As of 14 August 1997, 1302 tagged albacore (5.5% of the releases) had been recaptured and the tags returned to NMFS. Recaptures have been recorded from a wide range of national fleets and gear types, but the largest numbers of recaptures (68% of the total) were made by U.S. and Japanese baitboats and U.S. troll boats (Table 1). Recaptures occurred throughout the North Pacific, but most recaptures were concentrated in coastal waters adjacent to North America (mainly U.S. troll and baitboats) and west of 180° (Japanese baitboats) (Fig. 5).

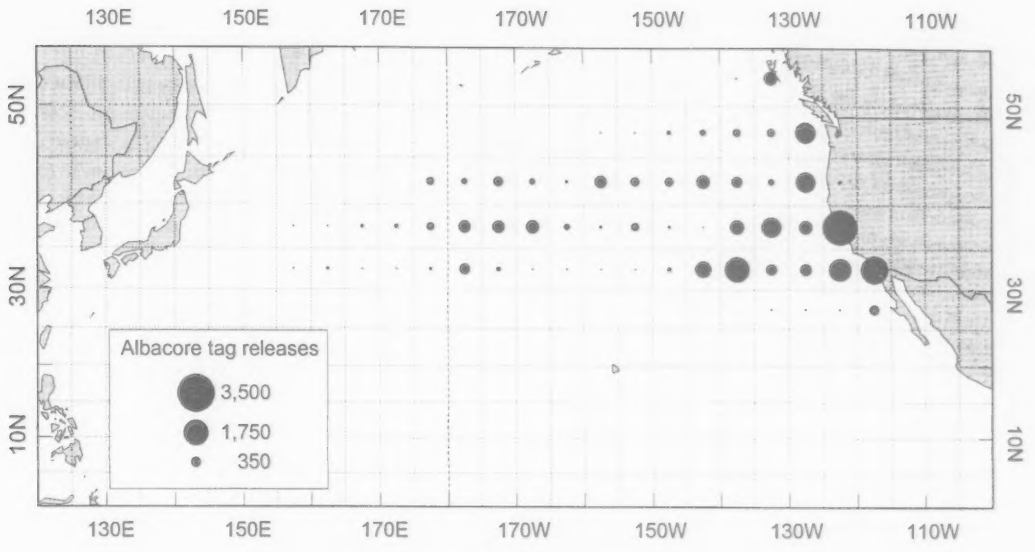


Figure 3
Geographical distribution of North Pacific albacore releases, 1971–89

Population dynamics model for tagged albacore

We used a tag-attrition model (e.g., Seber, 1973; Kleiber et al., 1987) to describe the dynamics of tagged albacore (hereafter referred to simply as "tags"). The model may be represented by

$$\hat{r}_{ijf} = R_i(1-\alpha)\beta\gamma \exp\left[-\sum_{k=1}^{j-1}\sum_f (F_{ikj}) - (j-1)(M+\psi)\right] \frac{F_{ijf}}{\sum_f F_{ijf} + M + \psi}\left[1-\exp\left(-\sum_f F_{ijf} - M - \psi\right)\right], \quad (1)$$

where $\hat{r}_{ijf}$ = the estimated number of tags from release group i recaptured by fleet f in time period j and returned with complete information (recapture time and fleet);
R_i = the number of tags released in release group i;
α = the proportion of type-1 tag losses;
β = the proportion of recaptured tags that are returned;
γ = the proportion of returned tags having complete information;
F_{ijf} = the instantaneous rate of fishing mortality on release group i in time period j by fleet f;
M = the instantaneous rate of natural mortality;
ψ = the instantaneous rate of type-2 tag loss;
i = an index for release group;
j = an index for time period;
k = an index for time periods prior to j; and
f = an index for fleet.

Data stratification

In order to allow seasonal variability in tag returns to be modeled, tag releases and returns were grouped by the quarter (Jan–Mar, Apr–Jun, Jul–Sep, and Oct–Dec) and year of release and recapture. This resulted in 48 release groups (Table 2). Small numbers of releases in 1994 and 1995, from which no recaptures have so far been reported, were not included in the analysis. We defined five fleets: 1) U.S. baitboat; 2) Japanese baitboat; 3) U.S. and Canadian troll (referred to as the troll fleet); 4) Japanese, Korean, and Taiwanese longline (referred to as the longline fleet); and 5) others (consisting of recapture sources not otherwise defined). This definition was designed to group fleets having similar characteristics (fishing methods, seasonal distributions of effort, and sizes of albacore caught). The observed tag returns, r_{ijf}, were thus grouped by tag release group (i), quarter and year of recapture (j), and recapture fleet (f). Tag returns to the end of 1992 were considered in the analysis.

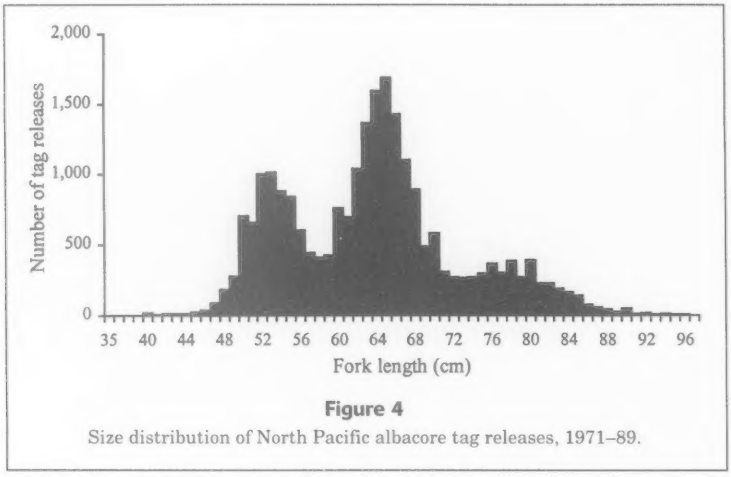


Figure 4
Size distribution of North Pacific albacore tag releases, 1971–89.

Table 1
Number of albacore tag returns in the North Pacific, 1971–1992, by recapture fleet.

Vessel or gear type	Nationality	Number of returns	%
Baitboat		715	56.3
	U.S.	403	
	Japan	312	
Troll		148	11.7
	U.S.	146	
	Canada	2	
Sport		137	10.8
	U.S.	135	
	Japan	2	
Longline		79	6.2
	Japan	61	
	Korea	15	
	Taiwan	2	
	Unknown	1	
Purse seine		39	3.1
	U.S.	34	
	Japan	4	
	Mexico	1	
Drift gill net		29	2.3
	U.S.	1	
	Japan	24	
	Canada	1	
	Taiwan	3	
Handline		5	0.4
	U.S.	5	
Unknown		117	9.2
	U.S.	112	
	Japan	2	
Unknown		3	
Total		1269	100.0

Nuisance parameters

We assumed that tag shedding was the only source of type-1 and type-2 tag loss and therefore used values for α and ψ of 0.12 and 0.0245 per quarter, respectively, based on analysis of double-tagging data (Laurs et al., 1976). There are no independent estimates of nonreporting of North Pacific albacore tags, although Kleiber and Baker (1987) stated that "nonreporting losses are small for the major fisheries that recovered the tags"; they assumed $\beta = 0.9$. We also made this assumption but tested the sensitivity of our results to values of β in the range 0.1 to 1.0. The value of γ(0.87) was estimated directly from the tag-return data.

Reparameterization of fishing mortality

To create sufficient degrees of freedom to enable a statistical estimation of parameters, the number of fishing mortality parameters to be estimated, F_{ijf} needs to be reduced. If we assume for the moment that F_{ijf} is independent of release group i, $F_{.jf}$ may be reparameterized as a function of fishing effort, E_{jf}, and catchability, q_{jf}:

$$F_{.jf} = q_{.f} E_{jf}. \quad (2)$$

We may then propose models that constrain q_{jf} in some sensible way. Let S_{jf} denote a matrix that contains, for each f, a season for each time period indexed by j. We tested two seasonal schemes: no seasonal variation for any fleet and seasonal variation (Q1=Jan–Mar, Q2=Apr–Jun, Q3=Jul–Sep, Q4=Oct–Dec) for all fleets.

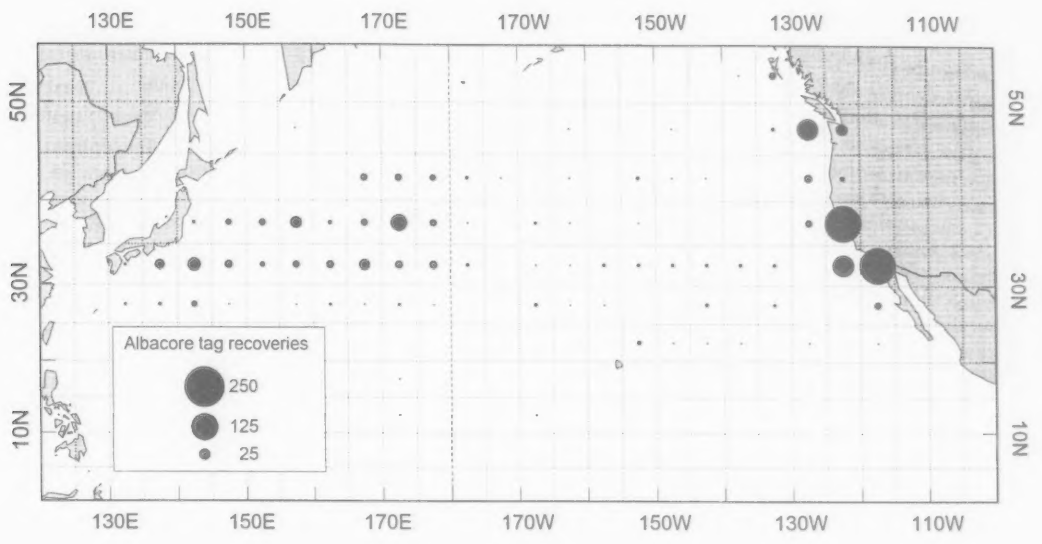


Figure 5
Geographical distribution of North Pacific albacore recoveries, 1971–92

Additionally, we tested constraints on q_{jf} that specified how catchability might vary over longer (multiyear) time periods. Let T_{jf} be a matrix that, for each f, maps time period j into a series of multiyear periods within which the seasonal pattern of catchability for that fleet may be assumed to be constant. We tested two schemes for T_{jf}: a constant pattern of catchability over time for all fleets and catchability patterns for all fleets specific to four time periods (1=1971 Q4 to 1974 Q4, 2=1975 Q1 to 1979 Q4, 3=1980 Q1 to 1984 Q4, and 4=1985 Q1 to 1992 Q4). Incorporating the notation for seasonal and multiyear effects, Equation 2 may then be rewritten as

$$F_{.jf} = q_{S_j T_j} E_{jf}. \quad (3)$$

Quarterly effort statistics for fleets 1 and 3 were obtained from NMFS databases. Statistics for fleets 2 and 4 were obtained from Secretariat of the Pacific Community databases. An arbitrary, constant level of effort was assumed for fleet 5. Effort data were compiled for the period from 1971 Q4 to 1992 Q4 to correspond to the period of the tagging experiment.

Changes in availability of the tagged population

The model as described thus far implies that the availability of the tagged population to the various fisheries remains constant for the duration of the experiment. There are two reasons why this assumption may not be satisfied, necessitating some adjustment to the model. First, the spatial distribution of the tagged population of any release set in relation to the spatial distribution of fishing effort by the recapture fleets was not constant over time. In particular, because most releases occurred in the eastern Pacific, the tagged population would have been initially more available to the U.S. baitboat and troll fleets and less available to the Japanese baitboat and longline fleets, which have a more westerly distribution. Over time, as the tagged population dispersed, the effects of such differential spatial availability would be expected to dissipate. Second, the availability of the tagged population to the recapture fleets would also be affected by the size distribution of the tagged population. Tagged fish at release were generally of a size similar to sizes of fish captured by the surface fisheries but were considerably smaller than those captured by the longline fishery. Therefore, the availability of the tagged population at release would not be limited initially by size for the surface fisheries but would be reduced for the longline fishery. As the tagged fish grew, their availability to the longline fishery would become less restricted by their size, but their availability to the surface fisheries might be reduced as they "grew out" of the size range typically exploited by those fisheries. Because our model has neither spatial nor size structure, the effects of size and spatial distributions cannot be explicitly incorporated. However, we developed an approximate means to allow for such effects in ag-

Table 2
North Pacific albacore tag-release and tag-return data, summarized by release group.

Releases			Returns						
			With recapture date						
Group	Date (qtr/yr)	Number	U.S. baitboat	Japan baitboat	Troll	Longline	Other	Recapture date unavailable	Total
1	4/71	887	13	6	1	0	7	6	33
2	2/72	1110	42	10	2	3	11	15	83
3	3/72	976	48	3	4	2	27	14	98
4	2/73	1611	50	19	10	2	4	22	107
5	3/73	182	1	2	0	0	1	1	5
6	4/73	12	0	0	0	0	0	0	0
7	2/74	1379	39	23	5	2	3	12	84
8	3/74	1006	31	36	2	4	2	8	83
9	4/74	101	1	2	1	0	3	1	8
10	2/75	406	1	6	0	0	5	1	13
11	3/75	902	39	10	9	2	23	16	99
12	4/75	41	2	0	1	0	1	1	5
13	2/76	449	7	1	1	0	5	3	17
14	3/76	1115	32	7	6	3	11	14	73
15	4/76	17	0	0	0	0	1	0	1
16	1/77	1	0	0	0	0	0	0	0
17	2/77	63	1	2	0	1	0	1	5
18	3/77	1725	22	18	20	5	35	13	113
19	4/77	273	3	0	2	3	3	2	13
20	2/78	236	0	11	1	3	2	1	18
21	3/78	2196	21	29	56	15	27	16	164
22	4/78	290	2	1	1	2	3	1	10
23	2/79	272	0	8	0	2	0	1	11
24	3/79	1451	8	21	11	7	9	8	64
25	2/80	199	0	0	0	0	0	1	1
26	3/80	897	1	18	0	1	8	4	32
27	4/80	19	0	0	0	0	1	0	1
28	1/81	56	0	0	1	0	0	0	1
29	3/81	189	0	1	1	1	3	1	7
30	1/82	13	0	0	1	0	0	0	1
31	2/82	173	0	1	0	0	2	0	3
32	3/82	991	0	22	0	2	7	1	32
33	4/82	23	0	0	0	0	0	0	0
34	2/83	463	0	9	0	5	3	0	17
35	3/83	584	1	15	2	1	3	1	23
36	4/83	14	0	0	0	0	0	0	0
37	2/84	558	0	8	0	2	1	0	11
38	3/84	382	0	4	0	2	3	1	10
39	4/84	8	0	0	0	0	0	0	0
40	2/85	452	0	3	0	0	3	0	6
41	3/85	331	0	1	0	0	1	0	2
42	4/85	2	0	0	0	0	0	0	0
43	2/86	502	0	3	0	1	1	1	6
44	3/86	619	0	1	0	0	3	3	7
45	2/87	63	0	0	0	0	0	0	0
46	3/87	94	0	0	0	0	0	0	0
47	3/88	6	0	0	0	0	0	0	0
48	3/89	110	0	0	0	1	0	1	2
Total		23,449	365	301	138	72	222	171	1269

gregate in order to reduce the potential bias in the other parameter estimates of interest. We defined a fleet-specific availability coefficient, $\phi_{t_{ij}f}$, where the index t_{ij} refers to the number of time periods at liberty of release group i in time period j. Equation (3) then becomes

$$F_{ijf} = \phi_{t_{ij}f} q_{s_{if}} T_{jf} E_{jf}. \quad (4)$$

$\phi_{t_{ij}f}$ is therefore a proxy variable related to time at liberty that we used to correct, in an approximate way, for the effects of changing availability of the tagged population over time. However, $\phi_{t_{ij}f}$ need not be estimated for all t_{ij}. Rather, ranges of t_{ij} may be specified for which the $\phi_{t_{ij}f}$ are considered to be constant at either 0 (completely unavailable) or 1 (fully available).

A scheme for constraining $\phi_{t_{ij}f}$ was devised from preliminary inspection of the data, and some knowledge of albacore dispersion (Laurs and Lynn, 1977), growth (Laurs and Wetherall, 1981), and gear selectivity (Bartoo and Holts, 1993) in the North Pacific (Table 3). The scheme provided three time periods for spatial mixing of tagged albacore with respect to the surface fishery fleets and the "other" fleet (which has characteristics similar to the surface fishery fleets), and eight time periods to allow recruitment of tagged albacore to the longline fishery. During these periods, $\phi_{t_{ij}f}$ was estimated from the data. We assumed that tagged albacore remain fully available to the longline fishery during the constrained period for ($\phi_{t_{ij}f}$ =1 for t_{ij}>8). For the surface fishery and "other" fleets, this may not be a good assumption, because these fishing methods may not have fully selected albacore of larger size (Bartoo and Holts, 1993). Therefore, we assumed that albacore were fully available during periods 4–11 after release ($\phi_{t_{ij}f}$ =1 for 3<t_{ij}<12) but were completely unavailable to these fleets after 15 time periods ($\phi_{t_{ij}f}$ =0 for t_{ij}>15).

Table 3

Scheme used to define variation in tagged albacore population availability. See text for definition of symbols.

	t_{ij} (quarters)			
Fleet	$\phi_{t_{ij}f}$ estimated	$\phi_{t_{ij}f}$ = 1	$\phi_{t_{ij}f}$ estimated	$\phi_{t_{ij}f}$ = 0
U.S. baitboat	1–3	4–11	12–15	>15
Japanese baitboat	1–3	4–11	12–15	>15
Troll	1–3	4–11	12–15	>15
Longline	1–8	>8	—	—
Other	1–3	4–11	12–15	>15

To allow for a gradual decline in availability during the intermediate period (11<t_{ij}<16), $\phi_{t_{ij}f}$ was estimated from the data.

Parameter estimation

We used a multinomial likelihood function to fit the various models to the tagging data. A derivation of the likelihood function as applied to tagging data is given in Kleiber and Hampton (1994). We minimized the negative log of this function to obtain the parameter estimates, i.e. by minimizing (omitting terms dependent only on the data)

$$-\sum_i \left[\left(R_i - \sum_k r_{ik} \right) \ln \left(1 - \frac{\sum_k \hat{r}_{ik}}{R_i} \right) + \sum_k r_{ik} \ln \left(\frac{\hat{r}_{ik}}{R_i} \right) \right], \quad (5)$$

where the k subscript indicates an individual recapture stratum (combining recapture period, fleet, and time at liberty dimensions). Minimization was carried out with a quasi-Newton routine (Otter Research, 1991). The variance-covariance matrix of the estimated parameters was estimated from the inverse of the Hessian matrix (Bard, 1974). The variance of quantities that are functions of the estimated parameters (such as exploitation rates) were determined by the delta method (Seber, 1973).

Results

Model fits

Eight different model formulations, based on different combinations of constant or variable availability, constant or seasonal catchability, and presence or absence of multiyear effects on catchability, were fitted to the North Pacific albacore tagging data. The total numbers of estimated parameters and the maximum log-likelihood function values for each fit are shown in Table 4. It is clear that the addition of variable availability, seasonal catchability, and multiyear effects on catchability all result in highly significant improvements in fit. The model incorporating all three effects, model 8, is suggested as the most appropriate of the tested models on the basis of likelihood-ratio tests (Kendall and Stuart, 1979). Model 6, which did not incorporate multiyear catchability effects, was the next preferred model.

Examples of plots of observed and predicted tag returns, aggregated over tag release groups, are shown in Figure 6 for model 2 and in Figure 7 for model 8. As expected, there are large discrepancies

Table 4

Maximum log-likelihood function values for alternative model formulations comprising constant (–) or variable (+) availability, constant (–) or seasonal (+) catchability, and absence (–) or presence (+) of multi-year effects on catchability.

Model number	Variable availability	Seasonal catchability	Multi-year effects on catchability	Number of parameters	Log likelihood
1	–	–	–	6	–9,511.2
2	–	+	–	19	–9,210.7
3	–	–	+	19	–9,386.1
4	–	+	+	50	–9,036.9
5	+	–	–	37	–9,089.9
6	+	+	–	47	–8,834.4
7	+	–	+	47	–8,973.3
8	+	+	+	79	–8,666.5

Table 5

Estimates of natural mortality rate M and $\phi_{t,f}$ obtained from fitting model 8 (see Table 4) to the North Pacific albacore tagging data. Underlined zeros indicate parameters set to zero because of zero tag return in those time periods.

	Recapture fleet											
	U.S. baitboat		Japan baitboat		Troll		Japan longline		Other			
Parameter	Estimate	CV	Estimate	CV	Estimate	CV	Estimate	CV	Estimate	CV	Estimate	CV
M (1 year)	0.608	0.090										
ϕ_{1f}			0.176	0.207	0.035	0.510	0.408	0.252	0.000	—	0.774	0.174
ϕ_{2f}			0.256	0.168	0.067	0.601	0.802	0.231	0.000	—	0.344	0.269
ϕ_{3f}			0.297	0.273	0.169	0.511	0.286	0.755	0.056	0.626	0.900	0.424
ϕ_{4f}									0.103	0.763		
ϕ_{5f}									0.000	—		
ϕ_{6f}									0.414	0.470		
ϕ_{7f}									0.306	0.406		
ϕ_{8f}									0.212	0.741		
ϕ_{12f}			0.277	1.012	0.299	0.398	1.000	—			0.654	0.731
ϕ_{13f}			0.415	0.594	0.554	0.469	0.313	1.015			0.290	0.723
ϕ_{14f}			0.486	0.470	0.237	1.018	0.000	—			0.679	0.600
ϕ_{15f}			0.000	—	0.260	1.016	0.000	—			0.000	—

between observed and predicted returns for model 2, particularly in the time periods soon after release. Major discrepancies were eradicated in the model 8 fit, which has greater flexibility in fitting the returns for these initial periods. Notice also that model 8 not only better predicts the returns for time periods in which $\phi_{t_0 f}$ was estimated (periods 1–8 for the longline fleet, periods 1–3 and 12–15 for all other fleets) but performs much better in predicting returns from periods of assumed full availability as well (e.g. periods 5 and 6 for U.S. baitboat and troll, periods 10–15 for longline).

Parameter estimates

Estimates of M and $\phi_{t_0 f}$ for the model 8 fit (β=0.9) are given in Table 5 by way of example. The model 8 estimate of M (0.608/yr, coefficient of variation 0.09) is similar to estimates obtained by Bertignac et al.[1] from albacore tagging data in the South Pacific but

[1] Bertignac M., P. Lehodey, and J. Hampton. 1996. An analysis of the South Pacific albacore tagging data: estimation of movement patterns, growth and mortality rates. 6th South Pacific Albacore Research Group meeting; 5–7 March 1996. [Available from senior author.]

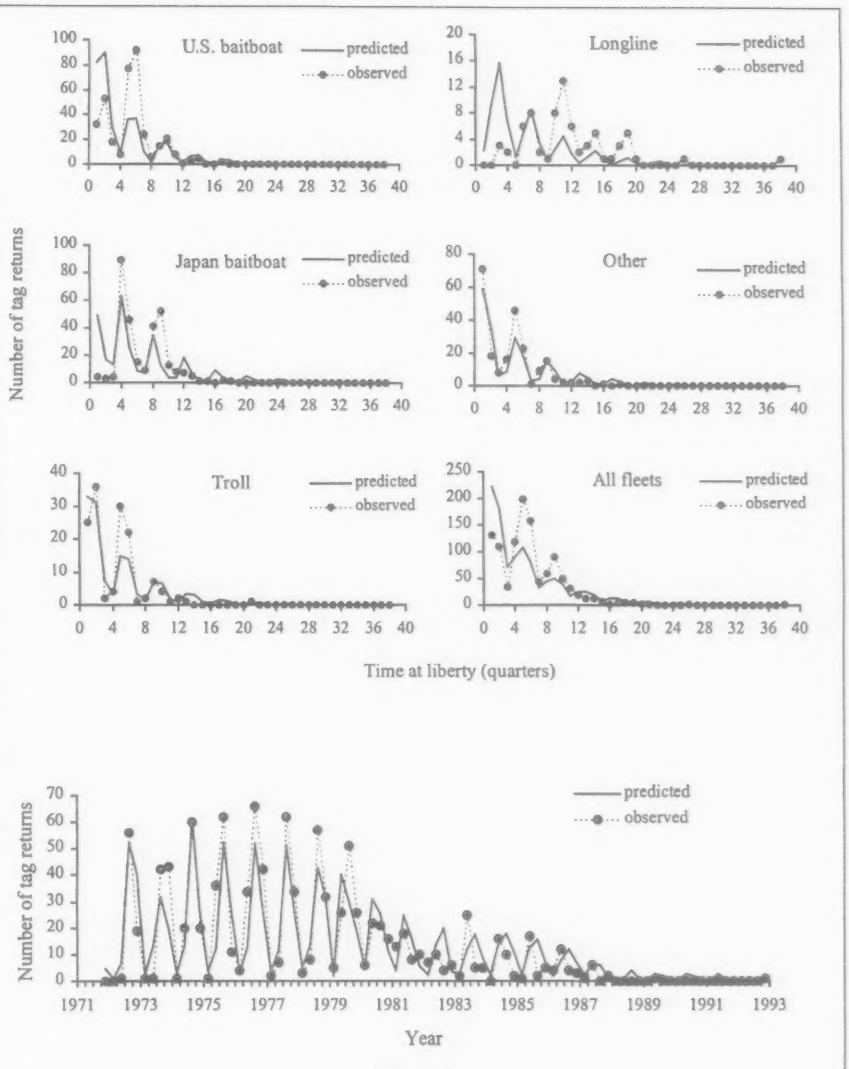


Figure 6

Observed tag return numbers and tag returns predicted with model 2 (see Table 4 for description).

higher than previous estimates obtained from fishery data by Suda (1966) and Fournier et al. (1998). Model 1–4 estimates of M (0.496–0.536/yr) are lower than those of models 5–8 (0.576–0.632/yr) because in the former, the models attempt to accommodate the low numbers of initial tag returns by depressing M, whereas in the latter, reduced availability for the initial time periods rather than reduced M is found to be a more likely solution. We noted that the correlation coefficients between the estimates of M and the $\phi_{t_0,f}$'s for the initial time periods were always negative and were in the range of –0.09 to –0.45.

The coefficients of variation of the $\phi_{t_0,f}$ estimates were variable (0.16–1.0) and were particularly high for the surface fleets at time periods at liberty beyond three years when very few tagged albacore were recovered.

For model 8, considerable differences in catchability estimates among time periods for all fleets were detected, although no consistent trends were evident (Fig. 8). The confidence intervals on these estimates were large in some cases.

Estimates of the total exploitation rate (percentage of the population harvested) in year y, calculated by

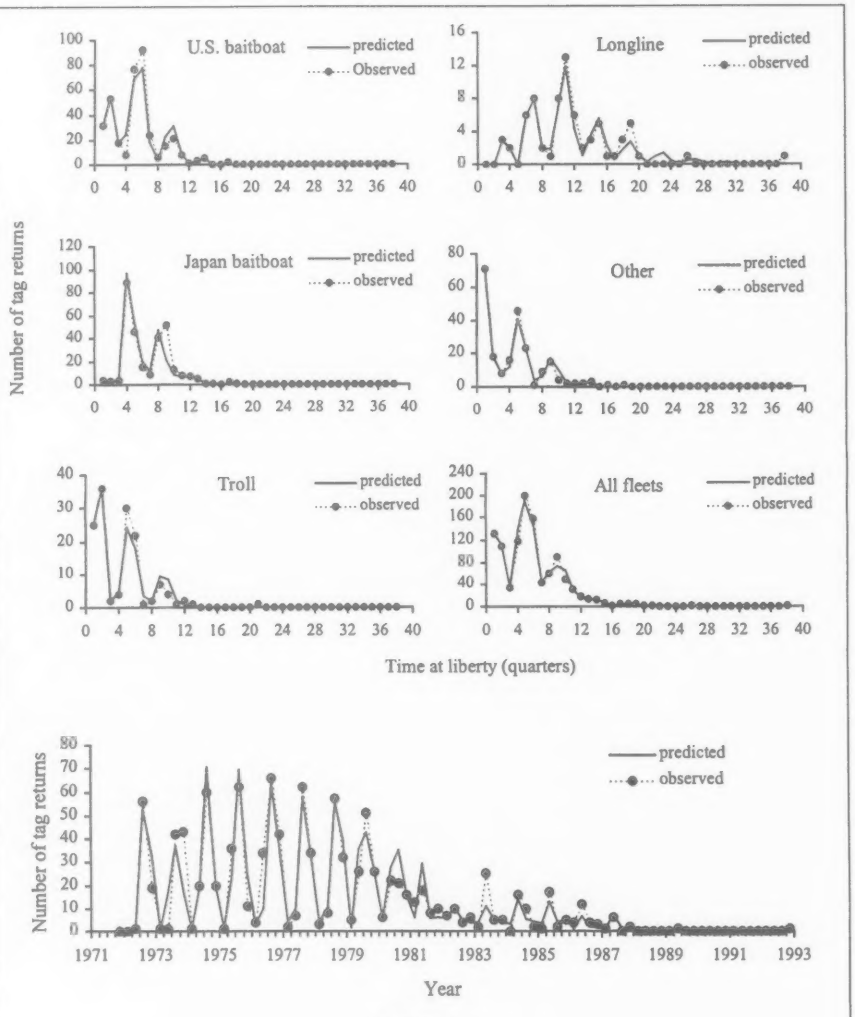


Figure 7

Observed tag return numbers and tag returns predicted with model 8 (see Table 4 for description).

$$\frac{\sum_f \sum_k q_{S_{kf} T_{kf}} E_{kf}}{\sum_f \sum_k q_{S_{kf} T_{kf}} E_{kf} + M} \qquad (6)$$

$$\left[1 - \exp\left(-\sum_f \sum_k q_{S_{kf} T_{kf}} E_{kf} - M\right)\right] \times 100\%,$$

where k is a quarter occurring in year y, are shown in Figure 9 (model 8, β=0.9). Estimated exploitation rate has been <10% for most of the time series; it declined between 1976 and 1988 and increased slightly afterwards.

Effect of assumed tag reporting rate

Although the tag-reporting rate is thought to have been high for North Pacific albacore (Kleiber and Baker, 1987), this contention is not supported by independent data. We therefore examined the sensitivity of the results to different values of β (assumed to apply equally to each fleet) for the model 8 fit. The estimates of M were directly related to β; conversely, average exploitation rate was inversely related to β (Fig. 10). In both cases, the sensitivity was slight for $\beta > 0.6$. If the tag-reporting rate was above this level for the main fleets, the results of our analysis should have been robust to small departures from the assumed value.

In the absence of other information, the tag-reporting rate was assumed to be constant over time. It is possible that reporting could have varied over time, owing to variation in the effectiveness of tag recovery procedures or cooperation of fishing fleets. Although it is not possible to test conclusively such hypotheses with the available data, we might note that the time-related variability in catchability estimated with model 8 (Fig. 8) could equally have been interpreted as variation in reporting rates, because catchability and reporting rate are highly correlated in these models.

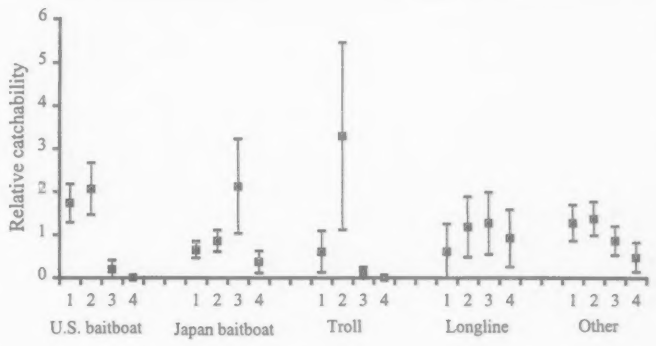


Figure 8

Estimated relative catchability (seasonally averaged and normalized within fleet categories) by multiyear time period, with 95% confidence intervals. 1=1971 Q4 to 1974 Q4, 2=1975 Q1 to 1979 Q4, 3=1980 Q1 to 1984 Q4, 4=1985 Q1 to 1992 Q4.

Discussion

The use of a tagged sample of the population to infer characteristics of the population in general is a common technique in fisheries stock assessment. For such inferences to be valid, several assumptions, discussed in detail by Seber (1973), need to hold. For North Pacific albacore, the assumption of equal probabilities of capture of tagged and untagged fish is likely to be critical. As noted earlier, both the spatial distribution of the tagged population in relation to recapture effort, and the size distribution of the tagged fish in relation to the size-selective characteristics of the different fishing gears are likely to result in violation of this assumption. We have developed a procedure to correct for these deficiencies in an approximate way. The procedure uses time-at-liberty information and knowledge of appropriate time lags to provide some correction for nonuniform availability of the tagged population to the various fishing fleets that is due to spatial and size effects. A more elegant approach would be to develop a model that explicitly deals with the spatial and size structure of the tagged population and with the spatial distribution and size selectivity of fishing effort. Spatially disaggregated tag models are now available (e.g. Kleiber and Hampton, 1994; Sibert et al., in press). An extension of such a model to include size or age structure would provide an improved method for analyzing the North Pacific albacore data.

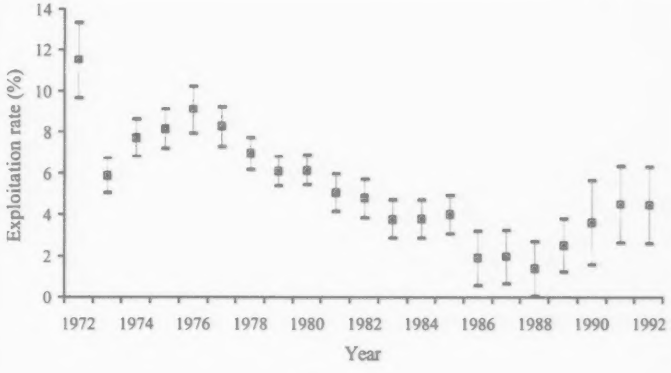


Figure 9

Time series and 95% confidence intervals of estimated annual exploitation rates of North Pacific albacore obtained for model 8 (see Table 4 for description).

The natural mortality rate parameter estimated from tagging data in this study is higher than some previous estimates for albacore. We have shown that M will be overestimated if the tag-reporting rate is overestimated. Although tag reporting for the major fleets is believed to have been high, it is possible that unreported tag recaptures by the drift gillnet fleet, which reported relatively few recaptures, have resulted in a positive bias in our estimate of M.

If the exploitation of tagged albacore is similar to exploitation of the North Pacific population in general, our results suggest that aggregate exploitation rates declined from the mid-1970s to 1988, after which some increase occurred. The results of our preferred model (model 8) further suggest that an-

nual total exploitation rates have been less than 10% during most of the years of the experiment. However, there is a strong indication that exploitation of tagged albacore by the troll fleet may not be representative of exploitation patterns generally by this fleet. The total number of tag returns from the troll fleet was 148 (Table 1). The U.S. baitboat fleet, which fished in an area similar to that fished by the troll fleet during the 1970s and 1980s, reported 403 tag recaptures. However, during the period of the tagging experiment, troll catches were some eight times baitboat catches (Liu and Bartoo, 1995). There is no ready explanation for this inconsistency. One possibility is that differential reporting rates existed between the fleets. However, given the earlier assertion that tag-reporting rates were high in general, differential tag reporting is unlikely to be the cause of such a discrepancy. Another possibility is that albacore become "hook shy" after they have been captured by trolling and are thereafter less likely to respond to trolled lures. Because the majority of albacore tag releases were troll-caught, such behavior would render the tagged population less available to the troll fleet than the albacore population in general. If this was indeed the reason for the paucity of troll-caught returns, relative availability of tagged albacore to the troll fleet would need to be of the order of 3.5% (compared with 100% for the U.S. baitboat fleet) to reconcile the tag-return and catch data for these fleets. Such reduced availability would result in significant underestimation of exploitation rates if not explicitly accounted for in the analysis. If we set $\phi_{tf} = 0.035$ for $3<t<16$ for the troll fleet, estimated exploitation rates that would apply to the untagged population are considerably higher, declining from around 40% in the 1970s to less than 10% since the mid-1970s (Fig. 11). At this point, we cannot be sure that the "hook shy" hypothesis is viable or not; therefore, both of the time series shown in Figure 11 should be considered as equally valid possibilities until additional information becomes available.

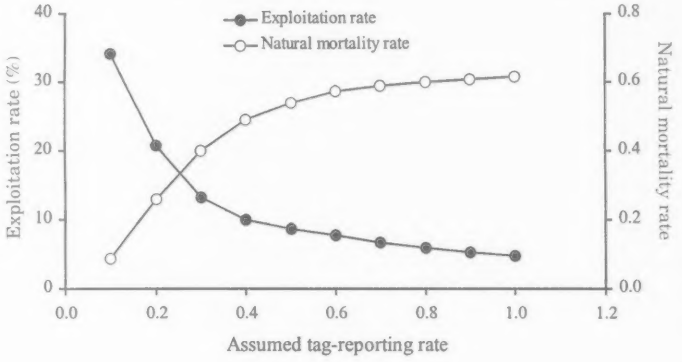


Figure 10

Estimates of annual natural mortality rate and annual average exploitation rate (total for all fleets) for model 8 (see Table 4 for description) as a function of the tag-reporting rate (β). The same value of β is assumed to apply to each fleet.

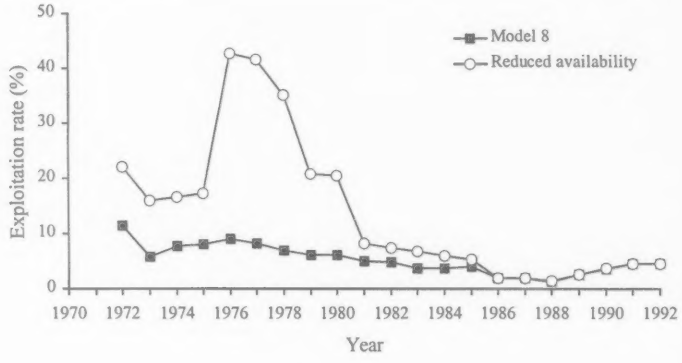


Figure 11

Estimates of annual exploitation rates of North Pacific albacore under hypotheses of full availability of tagged albacore to the troll fleet (model 8), and reduced availability due to "hook shyness."

Acknowledgments

We are grateful to Babera Kaltongga for assistance in compiling tagging and fishery data. Eric Prince and Joseph Powers provided valuable comments on an earlier version of the manuscript. The manuscript was improved by the comments of two anonymous reviewers.

Literature cited.

Bard, Y.
1974. Nonlinear parameter estimation. Academic Press, New York, NY, 341 p.

Bartoo, N., and D. Holts.
1993. Estimated drift gillnet selectivity for albacore *Thunnus alalunga*. Fish. Bull. 92:371–378.

Fournier D. A., J. Hampton, and J. R. Sibert.
1998. MULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore *Thunnus alalunga*. Can. J. Fish. Aquat. Sci. 56:2105–2116.

Kendall, M. G., and A. Stuart.
1979. The advanced theory of statistics. Vol. 2: Inference and relationship. Charles Griffin, London, 748 p.

Kleiber, P., A. W. Argue, and R. E. Kearney.
1987. Assessment of Pacific skipjack tuna (*Katsuwonus pelamis*) resources by estimating standing stock and components of population turnover from tagging data. Can. J. Fish. Aquat. Sci. 44:1122–1134.

Kleiber P., and B. Baker,
1987. Assessment of interaction between North Pacific albacore, *Thunnus alalunga*, fisheries by use of a simulation model. Fish. Bull. 85:703–711.

Kleiber, P., and J. Hampton.
1994. Modeling effects of FADs and islands on movement of skipjack tuna (*Katsuwonus pelamis*): estimating parameters from tagging data. Can J. Fish. Aquat. Sci. 51:2642–2653.

Laurs, R. M., W. H. Lenarz, and R. N. Nishimoto.
1976. Estimates of rates of tag shedding by North Pacific albacore, *Thunnus alalunga*. Fish. Bull. 74:675–678.

Laurs, R. M., and R. J. Lynn.
1977. Seasonal migration of North Pacific albacore, *Thunnus alalunga*, into North American coastal waters: distribution, relative abundance, and association with transition zone waters. Fish. Bull. 75:795–822.

Laurs, R. M., and J. A. Wetherall.
1981. Growth rates of north Pacific albacore, *Thunnus alalunga*, based on tag returns. Fish. Bull. 79:193–302.

Liu, H.-C., and N. Bartoo.
1995. Report of the fourteenth North Pacific albacore workshop, Taipei, Taiwan, Republic of China, April 10–14, 1995. National Taiwan University, Taipei, Taiwan, Republic of China, 39 p.

Murray, T.
1994. A review of the biology and fisheries for albacore, *Thunnus alalunga*, in the South Pacific Ocean. *In* R. H. Shomura, J. Majkowski, and S. Langi (eds.), Interactions of Pacific tuna fisheries, vol. 2, Papers on biology and fisheries, p. 188–206. FAO Fish. Tech. Pap. 336/2.

Nishikawa, Y., M. Honma, S. Ueyanagi, and S. Kikawa.
1985. Average distribution of larvae of oceanic species of scombroid fishes, 1956–1981. Far Seas Fish. Res. Lab. S Series 12, 99 p.

Otter Research.
1991. AUTODIF, a C++ array language extension with automatic differentiation for use in non-linear modeling and statistics. Otter Research Ltd. Box 265, Station A, Nanaimo, British Columbia, 102 p.

Seber, G. A. F.
1973. The estimation of animal abundance and related parameters. Griffin, London, 654 p.

Sibert, J. R., J. Hampton, D. A. Fournier, and P. J. Bills.
In press. Maximum likelihood estimation of large-scale movement parameters from tag release and recapture data with an application to seasonal movements of skipjack tuna, *Katsuwonus pelamis*. Can. J. Fish. Aquat. Sci..

Suda, A.
1966. Catch variations in North Pacific albacore—VI. The speculations about the influences of fisheries on the catch and abundance of the albacore in the north Pacific by use of some simplified mathematical models. Rep. Nankai Reg. Fish. Res. Lab. 24:1–14.

Use and success of composite square-mesh codends in reducing bycatch and in improving size-selectivity of prawns in Gulf St. Vincent, South Australia

Matt K. Broadhurst
South Australian Aquatic Sciences Centre
P.O. Box 120
Henley Beach, South Australia 5022, Australia
Present address: Universidade Federal Rural de Pernambuco-UFRPE
Departamento de Pesca
Laboratório de Oceanografia Pesqueira
Av. Dom Manuel de Mederios
S/n, Dois Irmãos, Recife-PE, Brazil, CEP:52.171-900
E-mail address: fhvhazin@truenet.com.br

Roger B. Larsen
University of Tromsø
Breivika, N-9037, Tromsø, Norway

Steven J. Kennelly
N.S.W. Fisheries Research Institute
P.O. Box 21
Cronulla, New South Wales 2230, Australia

Paul E. McShane
South Australian Aquatic Sciences Centre
P.O. Box 120
Henley Beach, South Australia 5022, Australia

Abstract.—In response to recent voluntary adoption of square-mesh codends by commercial prawn trawlers in Gulf St. Vincent, Australia, two new designs of composite square-mesh codends were investigated for their utility in 1) reducing the bycatch of fish and 2) improving size-selectivity of the targeted prawns. The two designs (termed the composite-square-2 and the composite-square-3 codends) comprised mainly large sections of 52-mm netting hung on the bar but had different hanging ratios, tapers, and small diamond-mesh sections. A strategically located panel of 85-mm netting was inserted on the bar into the tops of the anterior sections of each codend to allow small fish to escape. Simultaneous comparisons with a conventional diamond-mesh codend (control) showed that both square-mesh designs significantly reduced the incidental capture of commercially important fish (by up to 96.9%). The numbers of prawns (*Penaeus latisulcatus*) were significantly reduced in both composite square-mesh codends (by up to 12.1%) but there was no significant reduction in weights of prawns. There were no significant differences in the selectivity parameters for prawns between the two designs. The results are discussed in terms of the probable effects that the different square-mesh configurations had on escape of fish and size-selectivity of prawns.

Manuscript accepted 12 August 1998.
Fish.Bull. 97:434–448 (1999).

Traditionally configured prawn trawls contain small diamond-shaped meshes in the codend and are not particularly selective fishing gears. In addition to the targeted prawns, they often retain large quantities of nontarget organisms, collectively termed bycatch (for reviews see Andrew and Pepperell, 1992; Alverson et al., 1994). In many prawn-trawl fisheries, this bycatch consists of a diverse assemblage of small fish, cephalopods, and crustaceans, including prawns smaller than optimal commercial size. The mortality of large quantities of juveniles of commercially or recreationally important species, or both, is of major concern, because it may deleteriously affect the recruitment and biomass of stocks targeted by other fisheries. Regulating selectivity of trawls to the desired size of prawns at first capture will also help to optimize yield and maintain sustainability of prawn stocks.

During the past decade, many studies have attempted to improve selectivity of prawn-trawl fisheries by altering the codends of trawls. Most of these studies can be categorized into examinations of 1) bycatch reducing devices (BRDs) that facilitate the escape of unwanted fish (e.g. Watson et al., 1986; Broadhurst and Kennelly, 1997; Rogers et al., 1997); or 2) different sizes, shapes, and configurations of mesh that improve selectivity of the targeted species by reducing the bycatch of conspecifics (e.g. Karlsen

and Larsen, 1989; Tokai et al., 1990; Thorsteinsson, 1992; Tokai and Sakaji, 1993). However, to minimize biological impacts on bycatch and to promote ecologically sustainable fisheries, prawn trawls should be modified to address both these issues. Furthermore, it is essential that the prawn industry actively contributes towards the development of such designs so that they will be more readily accepted and adopted as part of commercial operations (Kennelly and Broadhurst, 1995).

In some prawn-trawl fisheries, industry has resisted gear modifications because of negative effects on gear performance (e.g. Renaud et al., 1993; Robins-Troeger et al., 1995). However, an inexpensive and simple modification that has been successfully tested and adopted in fish trawls in the North Atlantic involves changing only the configuration of mesh in the codend by hanging conventional diamond-shaped mesh on the bar (termed "square mesh") (e.g. Robertson and Stewart, 1988; Fonteyne and M'Rabet, 1992; Suuronen and Millar, 1992). Panels of square mesh have also been used successfully in prawn trawls to improve target-selectivity and to reduce the bycatch of juvenile fish. For example, in the Icelandic shrimp, *Pandalus borealis*, fishery, Thorsteinsson (1992) found that codends made entirely from square mesh effectively reduced the catches of small prawns (10–20% of catch) and 0-group gadoids. In New South Wales (NSW), Australia, Broadhurst and Kennelly (1996; 1997) showed that strategically located composite panels of square mesh (BRDs) in diamond-mesh codends effectively excluded large quantities of unwanted fish and there was no concomitant reduction in catches of the targeted prawns, *Penaeus plebejus*.

Through industry involvement in research, these sorts of results have facilitated the rapid endorsement and acceptance of designs in the respective fisheries and in some cases, in other fisheries sharing similar characteristics (e.g. similar gear configurations, target species, etc). An example of this type of transfer of technology recently occurred in the Gulf St. Vincent prawn-trawl fishery in South Australia. This fishery currently involves ten vessels targeting western king prawns, *Penaeus latisulcatus*; some legally retained bycatch comprising balmain bugs, *Ibacus* spp., and southern calamari, *Sepioteuthis australis* are also taken. Operators are restricted by means of a series of controls that include a minimum mesh opening of 45 mm in the codend and a limit of 34 nights of trawling each year. Although no formal studies have been undertaken to determine the selectivity of the conventional gear or to quantify bycatches, in recent years fishermen have suggested that the mesh size is too small and retains unacceptable proportions of juvenile prawns and fish. During the 1996–97 season, in an attempt to increase the mean sizes of prawns caught, fishermen designed and incorporated full square-mesh codends in all their trawls (see Fig. 1).

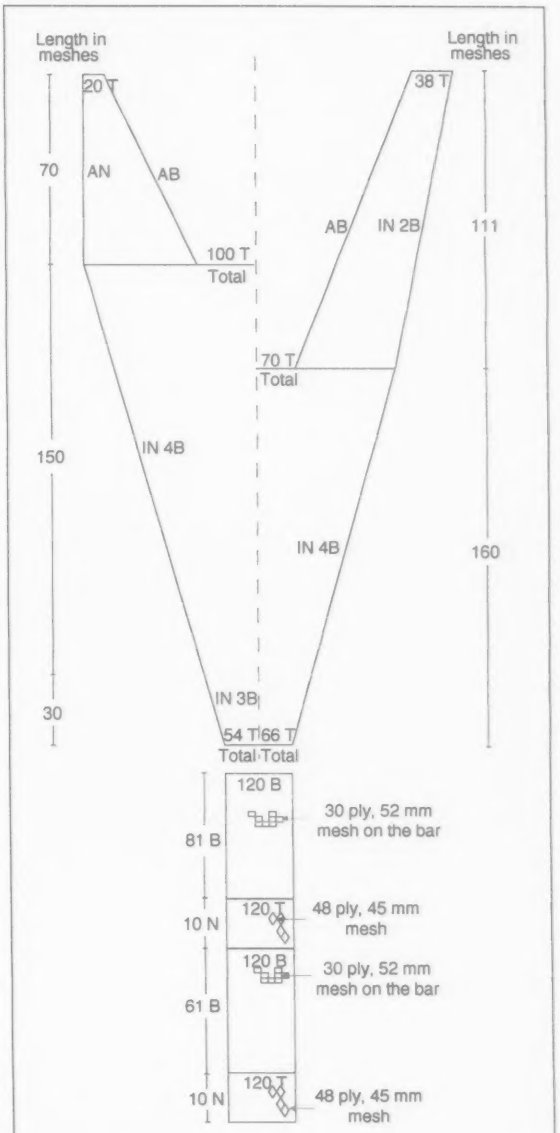


Figure 1

Diagrammatic representation of a "Gundry prawn trawl" and the industry developed "square-mesh-1 codend". T = transversals; N = normals; and B = bars.

Anecdotal reports from industry suggested that this codend (termed the "square-mesh-1 codend") re-

duced the bycatch of juvenile prawns and some small fish, although there were some concerns over suitable configurations of square mesh. Given that industry had already adopted the concept of using square mesh in codends, our aims in the present study were to modify the square-mesh-1 codend, after consultation with industry, so that it 1) incorporated a suitable BRD for unwanted fish and 2) increased the size-selectivity of targeted prawns.

Materials and methods

This study was done on commercial prawn-trawl grounds in Gulf St. Vincent, South Australia (Fig. 2), in November 1997, with a chartered commercial prawn-trawler (15 m). Three locally used prawn trawls (termed "Gundry trawls," Fig. 1), each with a headline length of 9.14 m were rigged in a standard triple gear configuration (see Andrew et al., 1991) and towed at 3 knots across a combination of sandy and light coral bottoms at depths ranging from 12 to 16.5 m. Each of the two outside trawls were rigged with zippers (Buraschi S-146R, pinlock sliders) to facilitate codend changes. The lengths of these zippers were calculated by assuming a fractional mesh opening of 0.35 (Broadhurst and Larsen, personal obs.) × the stretched mesh length × the mesh circumference. The middle net was not rigged in an identical manner to the outside trawls and therefore was excluded from any analysis.

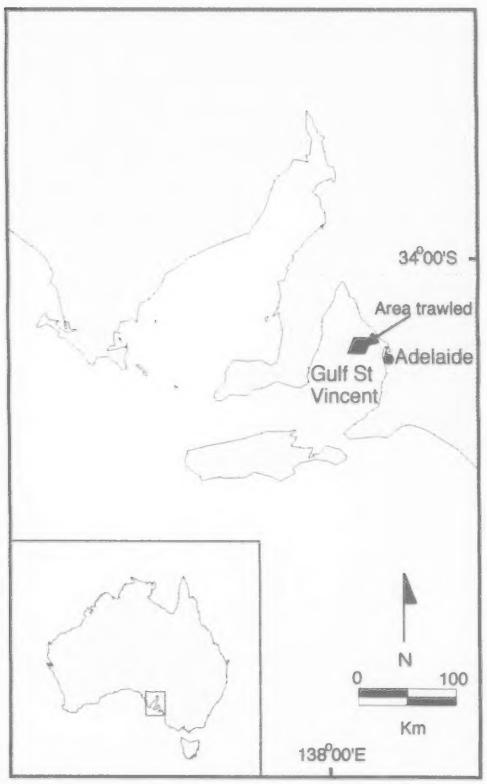


Figure 2
Location of Gulf St. Vincent and the area trawled.

Codends examined

Three codends, each attached to a zipper, were used in the experiment. The first codend, termed the control (Fig. 3A), represented conventional codends used prior to the 1996–97 fishing season and was made entirely of diamond-shaped meshes (45-mm mesh size, 2.35-mm diameter, 24-strand polyethylene twine), measuring 81 meshes in length and 100 meshes in circumference. The second and third codends (termed the composite-square-2 and composite-square-3 codends) comprised two sections of 52-mm mesh (400/36 ply, UV-stabilized, high-density polyethylene twine) cut on the bar. Each square-mesh section consisted of an upper and lower panel, sewn together so that knot directions were opposite. A panel of 85-mm netting (3-mm braided polyethylene twine), measuring 6 bars × 11 bars, was inserted into the tops of the posterior sections of each square-mesh codend starting approximately 1.1 m anterior to the last row of meshes (Fig. 3, B and C). This panel was positioned in a manner similar to that for the composite square-mesh panel used in NSW oceanic prawn trawls (see Broadhurst and Kennelly, 1996; 1997): that is, in an area of maximum displacement of water anterior to the end of the codend (to facilitate the escape of small fish, Broadhurst et al., 1999) but sufficiently in front of the anticipated build-up of catch.

The composite-square-2 codend comprised anterior and posterior square-mesh sections measuring 55 bars and 61 bars in length respectively. This codend was similar to the industry-developed square-mesh-1 codend, except that it had a circumference of 62 bars (1.6 m). The reduction in circumference from 120 bars (i.e. the industry design) to 62 bars was based on the expected fishing circumference of the normal diamond-mesh codend: that is, a fractional mesh opening (0.35) × the mesh size (45 mm) × the mesh circumference (100 T) = approx. 1.6 m. Two diamond-mesh 45-mm sections (mesh size, 400/48 ply UV-stabilized, high-density polyethylene twine), 10 meshes in length, and 100 meshes in circumference were inserted between the two square-mesh sections and immediately aft of the posterior square-mesh section (hanging ratio of 0.36) (Fig. 3B). The ante-

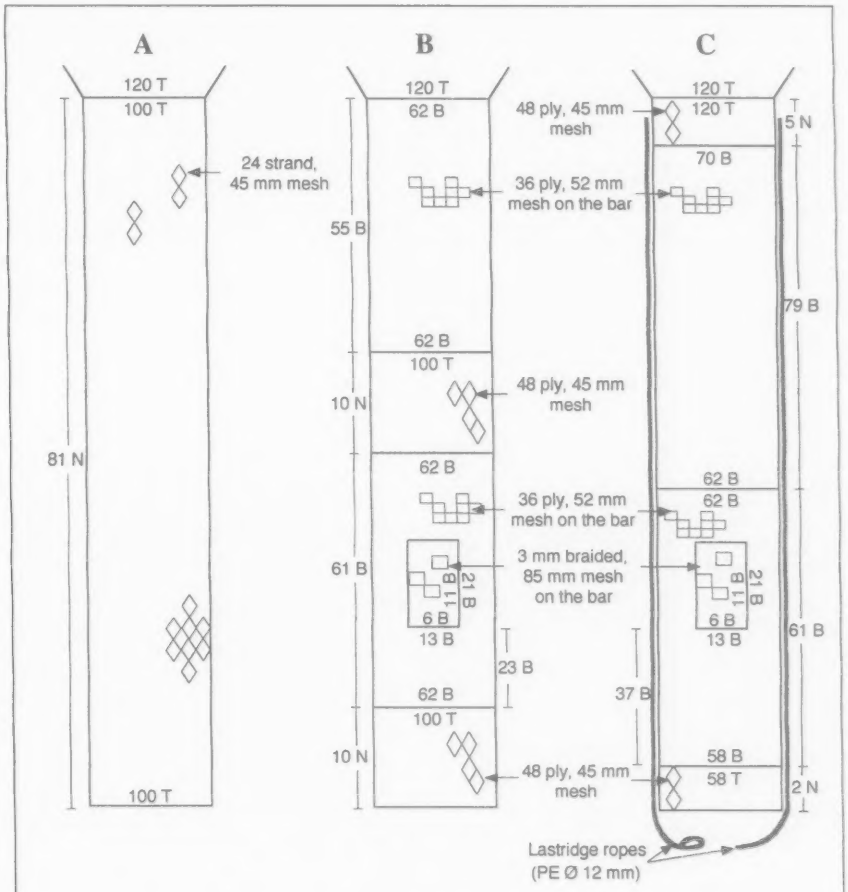


Figure 3

Diagrammatic representation of (**A**) the control codend, (**B**) composite-square-2 codend, and (**C**) composite-square-3 codend. T = transversals; N = normals; and B = bars.

rior diamond-mesh section was used to attach the codend lifting rope (termed "lazy-line"), whereas the posterior diamond-mesh section was used to attach the draw-string of the codend.

The composite-square-3 codend comprised an anterior square-mesh section 79 bars in length attached to a posterior square-mesh section 61 bars in length (Fig. 3C). The circumference of this codend tapered from 70 bars at the start of the anterior section to 58 bars at the end of posterior section. Two diamond-mesh sections (400/48 ply mesh size, UV-stabilized, high-density polyethylene twine), 2 meshes in length were attached immediately anterior and posterior (hanging ratio of 0.57) to the two square-mesh sections (Fig. 3C). The anterior diamond-mesh section measured 120 meshes in circumference, whereas the posterior diamond-mesh section measured 58 meshes in circumference and had the codend draw-string attached. Two 4.5-m lengths of 12-mm diameter, 3-strand polyethylene rope (termed "lastridge ropes") were firmly laced at a hanging ratio of approx. 0.9 to each of the two seams of the composite-square-3 codend to provide additional lengthwise strength to the entire codend. The posterior ends of the lastridge ropes extended past the codend and were secured together during each tow.

Sampling protocol and data collected

The two composite square-mesh codends were separately compared against the control codend. In each paired comparison, the control and composite square-mesh codend being tested were zipped to each outside trawl of the triple-rigged gear and towed simultaneously. The codends were used in normal com-

mercial tows of 45-min duration and randomly assigned after each tow (to eliminate biases between different trawls and sides of the vessel). The location of each tow was randomly selected from the available prawn-trawl locations that were possible under the fishing conditions. Over a total period of five nights, we initially completed 11 replicate tows of the composite-square-2 codend against the control. On the basis of results of this comparison and after discussions with representatives of industry, we then designed and constructed the composite-square-3 codend and immediately tested it against the control over another 11 replicate tows.

After each tow, the two codends were emptied onto a partitioned tray. Prawns and all individuals of commercially important species comprising bycatch were separated by species. The following categories of data were selected for each tow: the total weight of prawns and a subsample (100 prawns from each codend) of their lengths (to the nearest 1-mm carapace length); the total number of prawns (estimated from the weight of the subsample); the weights of total discarded bycatch, discarded noncommercial bycatch (i.e. species of no commercial value), and retained bycatch; the weights and numbers of commercially or recreationally (or both) important bycatch species; and the sizes (to the nearest 0.5 cm) of commercially or recreationally (or both) important fish. A random sample of prawns (approx. 14 kg) from each codend in each tow was separated and sent to A. Raptis & Sons PTY LTD (seafood processing plant) in Hindmarsh, Adelaide, where they were graded into commercial categories (number per pound) by a locally built automated "dynamic grading machine."

Several commercially important species were caught in sufficient quantities to enable meaningful comparisons. These were western king prawns, sand trevally, *Pseudocaranx wrighti*, red mullet, *Upeneichthys porosus*, school whiting, *Sillago bassensis*, Degen's leatherjacket, *Thamnaconus degeni*, southern sand flathead, *Platycephalus bassensis*, cuttlefish, *Sepia* spp., small-toothed flounder, *Pseudorhombus jenynsii*, and southern calamari.

Analysis of catch data

Data for all replicates that had sufficient numbers of each variable (defined as >2 individuals in at least 8 replicates) were analyzed with paired t-tests ($P \leq 0.05$). Except for the weights and numbers of prawns and small-toothed flounder, all variables were analyzed by using one-tailed tests of the hypothesis that the square-mesh codends caught less than the control. Although the composite square-mesh codends might have been expected to retain fewer prawns than the conventional diamond-mesh control codend (due to the larger square-shaped mesh), Broadhurst and Kennelly (1996; 1997) showed that trawls fitted with composite square-mesh panels caught more prawns than conventional trawls (possibly owing to a reduction in drag and a corresponding increase in swept area). Therefore, the weight and number of prawns were analyzed by using two-tailed tests. Catches of small-toothed flounder, a species that cannot pass through the square meshes, were also compared by using two-tailed tests. With the exception of data for catches of prawns, where analyses provided similar results for weights and numbers of variables, only data concerning numbers were included in Figure 4 to conserve space.

Size frequencies of commercially or recreationally (or both) important fish were plotted and compared with two-sample Kolmogorov-Smirnov tests (P=0.05), where there were sufficient data (n>25 in each codend, pooled across all tows).

Analysis of size-selectivity of prawns

The relatively large size of mesh used in the control (45-mm diamond mesh), compared with the composite square-mesh codends (52-mm mesh on the bar), meant that their selectivities overlapped. Insufficient numbers of smaller prawns were retained among individual hauls to enable analyses of between-haul variation (see Fryer, 1991). To provide sufficient data for analyses, size frequencies of prawns from each codend were combined across all tows. An estimated split model (Millar and Walsh, 1992) was used to fit logistic selection curves to these data by maximum likelihood method (Pope et al., 1975) by using the program "CC Selectivity" (Wileman et al., 1996). Logistic curve parameters, their standard errors, and 95% confidence limits were calculated for each codend. For each logistic curve, model deviance values were determined for a goodness-of-fit hypothesis (i.e. to test H_0: that the curves were logistic).

Size categories of commercially graded prawns from each codend were plotted and analyzed by using two-sample Kolmogorov-Smirnov tests (P=0.05). In these analyses, the numbers of prawns pooled across all samples from each codend were used for the degrees of freedom.

Results

Analysis of catch data

Compared with the control codend, both the composite-square-2 and composite-square-3 codends signifi-

cantly reduced the numbers of prawns caught (means reduced by 8.7% and 12.1%, respectively), with no significant reduction in weights (although the means were reduced by 1.8% and 3.7%, Fig. 4, A–B; Table 1). The weights of total discarded bycatch and discarded noncommercial bycatch were significantly reduced by 67.7% and 69.0%, respectively, in the composite-square-2 codend, whereas the composite-square-3 codend reduced these amounts by 58.4% and 54.2%. respectively (Fig. 4, C–D; Table 1). Both composite square-mesh codends significantly reduced the numbers and weights of sand trevally (by between 68.0% and 76.6%), red mullet, (by between 87.2% and 96.9%), school whiting (by between 90.6% and 96.9%), and southern sand flathead (by between 57.0% and 84.9%) (Fig. 4, E–H; Table 1). The composite-square-2 codend significantly reduced the mean number and weight of Degen's leatherjacket caught by 31.8% and 23.4%, respectively, and although not significant, these amounts were reduced by 24.6% and 20.8%, respectively, in the composite-square-3 codend (Fig. 4I; Table 1). There was also a significant reduction in the numbers of retained southern calamari, by 33.9% in the composite-square-3 codend (Fig. 4J; Table 1).

Two-sample Kolmogorov-Smirnov tests comparing the size-frequency distributions for fish measured from the control and composite square-mesh codends showed significant differences in the relative size compositions of sand trevally retained by both composite square-mesh codends and red mullet retained by the composite-square-2 codend (the control codend retained proportionally more larger fish, Fig. 5, A–B). No significant differences were detected in the size compositions of Degen's leather jacket retained in the composite square-mesh and control codends (Fig. 5C). There were insufficient data to analyze size-frequency distributions of school whiting and southern sand flathead.

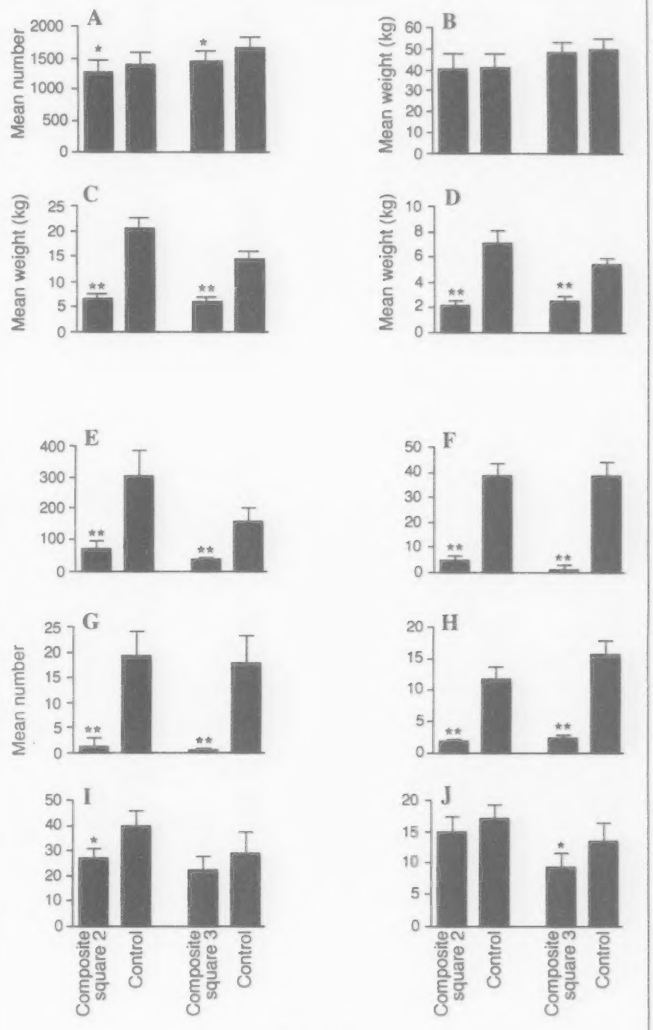


Figure 4

Differences in mean catches (per 45-min tow ± SE) between the composite square-mesh codends and control codend: the (**A**) numbers and (**B**) weights of king prawns (*Penaeus latisulcatus*); the weights of (**C**) total discarded bycatch and (**D**) discarded noncommercial bycatch; and the numbers of (**E**) sand trevally (*Pseudocaranx wrighti*), (**F**) red mullet (*Upeneichthys porosus*), (**G**) school whiting (*Sillago bassensis*), (**H**) southern sand flathead (*Platycephalus bassensis*), (**I**) Degen's leather jacket (*Thamnaconus degeni*), and (**J**) southern calamari (*Sepioteuthis australis*). ** = significant ($P<0.01$); * = significant ($P<0.05$).

Analysis of size-selectivity of prawns

The raw data, observed selectivity, and calculated logit values for prawns captured in the codends are listed in Table 2. Figure 6 shows the corresponding logistic length selection curves derived for each composite square-mesh codend. Model deviance indicated sufficient goodness of fit for both of these selection curves (Table 3; Fig. 7) although some size classes

Table 1

Summaries of paired *t*-tests comparing composite square-mesh and control codends. Weights and numbers of prawns and small-toothed flounder were analyzed with a two-tailed paired *t*-tests, whereas the remaining variables were analyzed with one-tailed paired *t*-tests. *n* = number of replicates; disc = discarded; noncomm = noncommercial. Significant *P*-values are in bold.

	Composite-square-2 versus control			Composite-square-3 versus control		
	Paired *t*-value	*P*	*n*	Paired *t*-value	*P*	*n*
No. of prawns	2.574	**0.027**	11	2.853	**0.017**	11
Wt. of prawns	0.648	0.531	11	0.915	0.382	11
Wt. of total disc bycatch	6.521	**0.0001**	11	6.662	**0.0001**	11
Wt. of disc noncomm bycatch	5.251	**0.0002**	11	6.051	**0.0001**	11
Wt. of retained bycatch	–0.424	0.659	11	0.947	0.183	11
No. of sand trevally	3.345	**0.003**	11	3.719	**0.002**	11
Wt. of sand trevally	4.016	**0.001**	11	4.050	**0.001**	11
No. of red mullet	6.901	**0.0001**	11	6.728	**0.0001**	11
Wt. of red mullet	6.927	**0.0001**	11	8.033	**0.0001**	11
No. of school whiting	6.912	**0.0001**	11	5.111	**0.0003**	10
Wt. of school whiting	4.887	**0.0003**	11	4.896	**0.0004**	10
No. of Degen's leatherjacket	2.442	**0.017**	11	1.378	0.099	11
Wt. of Degen's leatherjacket	1.945	**0.040**	11	1.139	0.140	11
No. of southern sand flathead	5.470	**0.0002**	11	6.328	**0.0001**	11
Wt. of southern sand flathead	5.487	**0.0002**	11	3.585	**0.0025**	11
No. of cuttlefish	1.247	0.122	10	1.037	0.163	10
Wt. of cuttlefish	1.217	0.127	10	0.792	0.224	10
No. of small-toothed flounder	–0.882	0.407	8	1.537	0.163	9
Wt. of small-toothed flounder	0.940	0.378	8	0.208	0.779	9
No. of southern calamari	0.772	0.229	11	3.123	**0.005**	11
Wt. of southern calamari	–0.576	0.711	11	–0.179	0.568	11

had high deviance residuals (Fig. 7, see also Appendix). Although all selectivity parameter estimates were slightly greater in the composite-square-3 codend, the 95% confidence limits for these estimates indicated that there were no statistically significant differences between the two modified codends.

Two-sample Kolmogorov-Smirnov tests comparing the commercial size compositions of prawns retained in each codend showed significant differences between the composite square-mesh and control codends (Fig. 8). Both composite square-mesh designs caught proportionally more larger prawns (<9/12 per pound) and fewer smaller individuals (>16/20 per pound).

Discussion

The work described in this paper illustrated the effectiveness of a strategically located panel of square mesh in codends for reducing catches of juvenile fish (see also Robertson and Stewart, 1988; Fonteyne and M'Rabet, 1992; Briggs, 1992; Broadhurst and Kennelly, 1996, 1997) and quantified, for the first time in commercial penaeid prawn-trawls, the utility of large panels of square mesh for improving the size-selectivity of the targeted prawns.

The composite square-mesh codends were equally effective in excluding large quantities of small individuals of fusiform species, including sand trevally, red mullet, school whiting, and southern sand flathead and there was no significant reduction in weights of prawns or total retained bycatch (Fig. 4; Table 1). Although the square mesh used throughout the main sections of both codends may have been large enough to permit some smaller fish (e.g. red mullet) to escape, the differences in the sizes of many fish retained between the composite square-mesh codends and the control (Fig. 5) indicated that to achieve the significant and quite large reductions in catch, most fish probably escaped through the larger 85-mm mesh panel located in the tops of the posterior sections of the codends.

The escape of large numbers of these individuals through the 85-mm square-mesh panel in both codends may be attributed to the influences of water

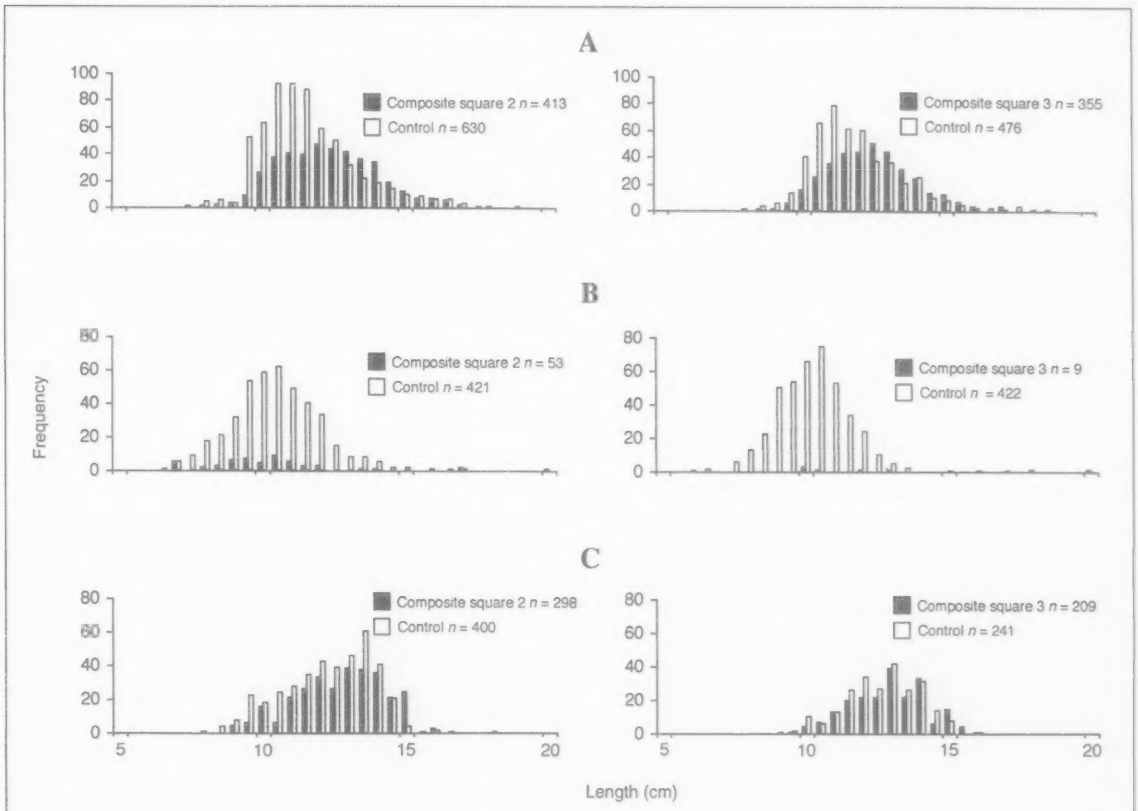


Figure 5

Size-frequency distributions of the composite square-mesh codends and control codend for (**A**) sand trevally (*Pseudocaranx wrighti*), (**B**) red mullet (*Upeneichthys porosus*), (**C**) Degen's leatherjacket (*Thamnaconus degeni*), (**D**) school whiting (*Sillago bassensis*), and (**E**) southern sand flathead (*Platycephalus bassensis*).

flow anterior to the catch. The location of the panel (approx. 1.1 m from the end of the codend, Fig. 3) was based on a similar design (termed the composite square-mesh panel) that is currently used commercially in oceanic prawn trawls in NSW where it has been shown to be very effective in reducing the bycatch of large numbers of small fish (Broadhurst and Kennelly, 1996, 1997). In previous experiments, Broadhurst and Kennelly (1996) and Broadhurst et al. (1999) determined that at this position, there is some displacement of water forwards owing to the twine area and build-up of catch in the posterior section of the codend. Because small fish are probably using anaerobic muscle power to maintain position in the moving trawl and are quite fatigued when they enter the codend, this displaced water may be sufficient 1) to assist them to swim forwards and out through the larger meshes in the panel; and (or) 2) to enable them to reduce their tail-beat frequencies and maintain their position in the vicinity of the larger mesh for a longer period, increasing their chances of randomly escaping. The extent to which such a flow facilitated the escape of fish in the present study probably depended on their relative size or physiology (or both), because these factors largely influence swimming speed and endurance (Beamish, 1978). For example, the bycatch of fast-swimming species, such as sand trevally, and relatively large individuals of school whiting and southern flathead was greatly reduced in the two modified designs. However, although statistically significant, there was only a 30% reduction in the numbers of the relatively small Degen's leather jackets in the composite-square-2 codend and a lower nonsignificant 24% reduction in the composite-square-3 codend (Fig. 4I; Table 1).

A possible explanation for the significant reduction of Degen's leather jacket from the composite-square-2 codend may be the configuration of mesh

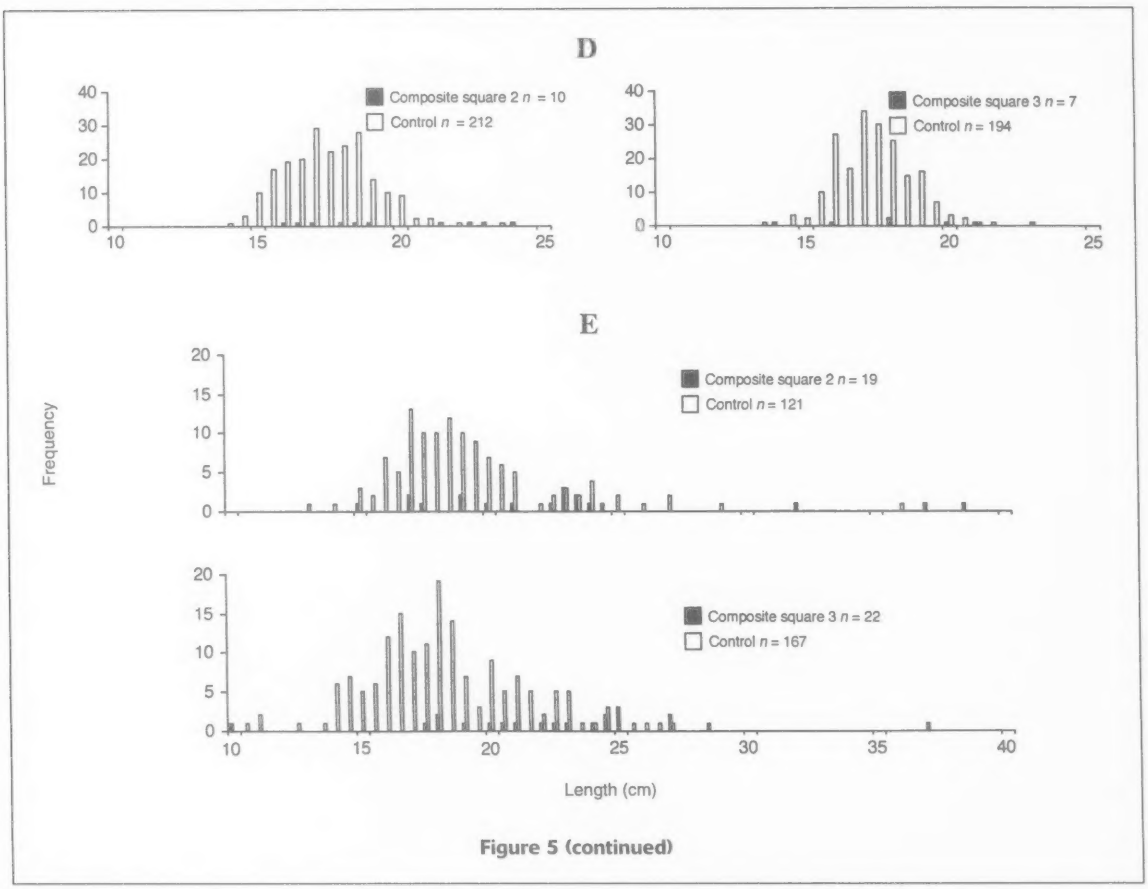


Figure 5 (continued)

used in the posterior section of the codend and the effects that this had on distribution of catch and water flow. Because the posterior diamond-mesh section in this codend was 10 meshes in length, 100 meshes in circumference, and attached to a square-mesh section 62 bars in circumference (hanging ratio of 0.36), as the catch increased it would have spread laterally, increasing its surface area that was incidental to the flow and, therefore, increasing the displacement of water forwards (see Broadhurst and Kennelly, 1996, 1999). The composite-square-3 codend, however, was designed to increase size-selectivity of prawns and was tapered to a circumference of 58 bars attached to a posterior diamond-mesh section that was 2 meshes in length and only 58 meshes in circumference (hanging ratio of 0.57). Combined with lastridge ropes, this configuration would have forced a much smaller codend diameter than in the composite-square-2 codend, restricting any lateral distribution of catch. Any consequent reduction in surface area that was incidental to the flow and displacement of water forwards in this codend (which would limit any assistance to swimming fish) may account for the nonsignificant reduction of Degen's leather jackets and the poorer exclusion of small individuals comprising discarded noncommercial bycatch (Fig. 4D). It should be noted, however, that these results were based on only 11 tows and that further experiments may be required to provide additional evidence to either support or refute the hypothesis discussed above.

Although the mesh configuration and water flow in the composite-square-2 codend may have contributed to the escape of slightly more fish, in terms of optimizing sizes of prawns retained, the composite-square-3 codend appeared to be a better design. Although the 95% confidence limits about the selectivity parameters indicated no significant differences between the two designs (Fig. 6; Table 3), there was some evidence to suggest that the composite-square-3 codend did appear to select slightly more commercial-size prawns. For example, compared with the control, this codend caught significantly fewer prawns by number (difference between means of

Table 2

Length-frequency distributions (pooled across all tows) for prawns captured in the composite square-mesh and control codends, the observed selectivity (ratio of catches), and the fitted logit values. Carapace length in mm; CS2 = composite-square-2 codend; CS3 = composite-square-3 codend.

Carapace length	CS2 codend	Control codend	Observed selectivity	Logit value	CS3 codend	Control codend	Observed selectivity	Logit value
15	0	0	0.00	0.019	0	0	0.00	0.002
16	0	2	0.00	0.025	0	0	0.00	0.003
17	0	0	0.00	0.032	0	0	0.00	0.005
18	0	0	0.00	0.041	0	2	0.00	0.007
19	0	3	0.00	0.052	0	2	0.00	0.009
20	0	3	0.00	0.066	0	2	0.00	0.013
21	0	5	0.00	0.084	0	4	0.00	0.019
22	1	10	0.10	0.106	0	11	0.00	0.026
23	2	7	0.28	0.133	0	7	0.00	0.036
24	0	4	0.00	0.165	0	10	0.00	0.050
25	1	4	0.25	0.204	2	5	0.40	0.068
26	1	6	0.17	0.249	1	8	0.12	0.093
27	4	10	0.40	0.301	0	0	0.00	0.126
28	6	8	0.75	0.357	1	7	0.14	0.169
29	5	10	0.50	0.418	1	2	0.50	0.222
30	10	13	0.77	0.482	4	16	0.25	0.285
31	18	27	0.67	0.546	8	25	0.32	0.359
32	34	42	0.81	0.609	24	27	0.89	0.440
33	43	56	0.77	0.668	48	48	0.10	0.525
34	60	77	0.78	0.723	61	74	0.82	0.608
35	87	96	0.91	0.771	76	112	0.68	0.685
36	116	125	0.93	0.813	105	147	0.71	0.753
37	109	98	1.11	0.849	118	111	1.06	0.811
38	81	77	1.05	0.879	92	62	1.48	0.857
39	60	57	1.05	0.904	63	51	1.23	0.894
40	58	49	1.18	0.924	66	44	1.50	0.922
41	48	48	1.00	0.940	62	49	1.26	0.943
42	53	57	0.93	0.953	63	56	1.12	0.959
43	56	55	1.02	0.964	76	50	1.52	0.970
44	44	39	1.13	0.972	57	46	1.24	0.979
45	31	33	0.94	0.978	32	41	0.78	0.985
46	26	23	1.13	0.983	33	30	1.10	0.989
47	33	18	1.83	0.987	34	18	1.89	0.992
48	33	21	1.57	0.989	29	20	1.45	0.994
49	15	25	0.60	0.992	14	16	0.87	0.996
50	17	10	1.70	0.994	17	9	1.89	0.997
51	13	7	1.86	0.995	12	10	1.20	0.998
52	8	3	2.67	0.996	7	7	1.00	0.999
53	9	2	4.50	0.997	1	5	0.20	0.999
54	9	2	4.50	0.998	2	1	2.00	0.999
55	2	1	2.00	0.998	5	4	1.25	0.999
56	2	2	1.00	0.999	5	3	1.66	0.999
57	4	7	0.57	0.999	2	3	0.67	0.999
58	1	1	1.00	0.999	1	0	0.00	0.999
59	2	0	0.00	0.999	0	1	0.00	0.999
60	0	0	0.00	0.999	1	0	0.00	0.999
61	0	0	0.00	0.999	1	1	1.00	0.999

Table 3

Computed selectivity parameters for prawns (carapace length in mm) from the two composite square-mesh codends and deviance values for logistic curve goodness-of-fit. Standard errors are given in parentheses. a, b = logistic parameters (Pope et al., 1975). P = split proportion from estimated split model (Millar and Walsh, 1992).

	Composite-square-2 codend		Composite-square-3 codend	
a	−7.803		−11.079	
b	0.257		0.338	
P	0.544		0.562	
		95% confidence limits		95% confidence limits
25% retention (L_{25})	26.02 (1.19)	20.14–30.94	29.46 (0.76)	25.42–33.07
50% retention (L_{50})	30.28 (1.19)	28.13–33.38	32.71 (0.82)	31.29–34.59
75% retention (L_{75})	34.56 (1.76)	29.73–42.20	35.95 (1.13)	32.38–40.91
Selection range (SR)	8.53 (0.6)	4.89–12.16	6.49 (0.5)	4.21–8.76
Deviance	32.48		46.54	
df	39		40	
P-value	0.760		0.221	

12.1%) than did the composite-square-2 codend (difference between means of 8.1%), and there was no significant reduction in weights (Fig. 4; Table 1).

These slight differences in size-selectivity of prawns may be explained in terms of the behavior of prawns in the codend and the different configurations of mesh discussed above. Previous studies have shown that the response of prawns to stimuli from the trawl is minimal and after initial contact with the leading edge of the footrope, the prawns are quickly forced into the rear of the codend (Lochhead, 1961; Watson, 1976). Their escape at this point is primarily determined by their probability of randomly encountering openings between meshes that are large enough to pass through. In the composite-square-2 codend, the hanging ratio between the posterior diamond and square-mesh sections would have restricted the fractional diamond-mesh openings, limiting the opportunity for escape. Further, as the catch increased and spread laterally, this would have widened the diameter of the posterior section, providing prawns with less opportunity of encountering any open meshes in the sides of the codend. In contrast, we designed the composite-square-3 codend, so that it would assume a smaller diameter and circumference during fishing, but with a greater area of square mesh, thereby providing more opportunity for prawns to randomly encounter the sides of the codend and the open square meshes.

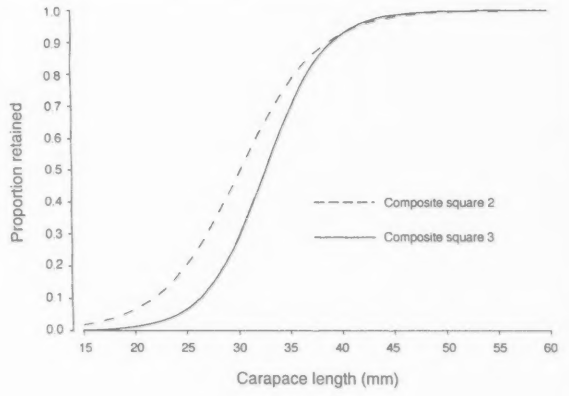


Figure 6

Size-selectivity curves for king prawns (*Penaeus latisulcatus*) from the composite square-mesh codends.

The results obtained in this study showed that composite square-mesh codends in penaeid prawn trawls can improve size-selectivity of the targeted prawns while reducing large quantities of unwanted fish. It is also apparent, that such modifications may improve the overall efficiency of the trawl in terms of increasing catches of prawns. For example, although the composite-square-2 and square-3 codends significantly reduced the numbers of prawns caught by 8.7% and 12.1%, compared with the control, the differences in weights of prawns were much smaller, to the point where they were nonsignificant (e.g. 1.8% and 3.7%, respectively). To achieve such a result, the two trawls containing composite square-mesh codends caught more prawns but retained mainly larger-size individuals.

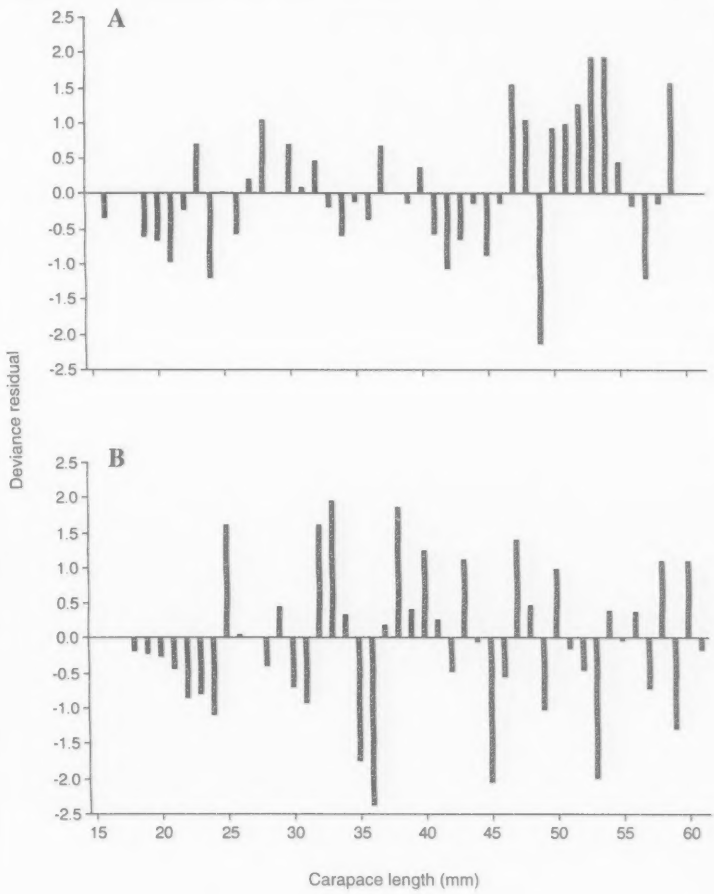


Figure 7

Plots of the deviance residuals from selection curves for the (**A**) composite-square-2 codend and (**B**) composite-square-3 codend.

One hypothesis to explain this result is that the large, open, square meshes in the composite square-mesh codends, combined with the overall size of the codends (approx. 4 m in length) allowed a faster release of water from the body of the trawl than did the control. Such an increase in flow may have resulted in prawns quickly passing into the codend after initial contact with the footrope, with less chance of randomly escaping over the headrope or out through the mouth of the trawl. In support of this, Walsh et al., (1992) provided evidence of similar flow-related effects on the catches of fish (American plaice, *Hippoglossoides platessoides*) from trawls fitted with square-mesh codends. In the present study, however, any potential effects of increased flow did not appear to influence fish such as small-toothed flounder (the only species that could not pass through the square mesh), because there were no significant differences in the catches between the composite square-mesh and control codends (Table 1). An alternative hypothesis proposed by Broadhurst and Kennelly (1997) to describe a similar increase in catches of prawns from NSW oceanic prawn trawls containing codends with composite square-mesh panels is that by reducing the weight of bycatch and therefore the drag in the codend, trawls with the composite square-mesh achieved slightly more swept area than did controls, thereby covering more of the sea bed and capturing more prawns.

Regardless of the underlying mechanisms, the increase in catches of target-size prawns, combined with the substantial reductions in the bycatch of fish,

led to unanimous industry acceptance and adoption of the composite-square-3 codend within two weeks of the conclusion of the field work described in this paper. Fishermen have since reported that the codend has minimal distortion (due to the lastridge ropes), allows increased tow duration, and provides an improved quality of prawns. These results illustrate the benefits that can be derived through liaison with industry and by incorporating their ideas into modifications to improve the selectivity of prawn trawls. Such voluntary adoption should ensure the continued development and refinement of designs, as part of normal commercial operations.

Acknowledgments

Funding for this work was provided by the Australian Fishing Industry Research and Development Corporation. We are grateful to Jim Raptis (A. Raptis & Sons PTY LTD) and Yvonne Aston for the use of their vessel *Jillian Sandra*. Thanks are extended to Geoff Gordon, Bruce Jackson, Kim Redman, Sam Tudorvic, Micheal Aston, Bill Walsh, Les Lowe (Gulf Net Mending PTY LTD), Hec Kavenagh, and all Gulf St. Vincent prawn-trawlers for their advice, assistance, and support. We would also like to acknowledge the Norwegian Research Council for their contribution to the involvement of Roger Larsen in this work.

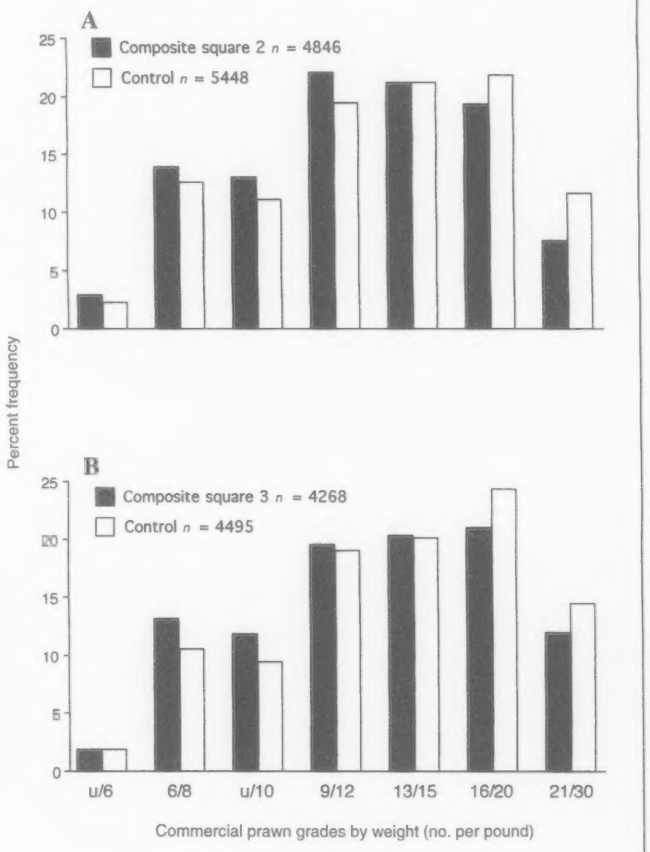


Figure 8

Commercial size categories of king prawns (*Penaeus latisulcatus*) caught with the (**A**) composite-square-2 and control codends and (**B**) composite-square-3 and control codends (u=under).

Literature cited

Alverson, D. L., M. H. Freeberg, S. A. Murawski, and J. G. Pope.
1994. A global assessment of fisheries bycatch and discards. FAO Fish. Tech. Paper 339, Rome, 233 p.

Andrew, N. L., K. J. Graham, S. J. Kennelly, and M. K. Broadhurst.
1991. The effects of trawl configuration on the size and composition of catches using benthic prawn trawls off the coast of New South Wales, Australia. ICES J. Mar. Sci. 48:201–209.

Andrew, N. L., and J. G. Pepperell.
1992. The by-catch of shrimp trawl fisheries. Oceanogr. Mar. Biol. Annu. Rev. 30: 527–565.

Beamish, F. W. H.
1978. Swimming capacity. *In* W. S. Hoar and D. J. Randall (eds.), Fish physiology, vol. VII, Locomotion, p. 101–187. Academic Press, New York, NY.

Briggs, R. P.
1992. An assessment of nets with a square mesh panel as a whiting conservation tool in the Irish Sea *Nephrops* fishery. Fish. Res. 13:133–152.

Broadhurst, M. K., and S. J. Kennelly.
1996. Effects of the circumference of codends and a new design of square-mesh panel in reducing unwanted by-catch in the New South Wales oceanic prawn-trawl fishery, Australia. Fish. Res. 27:203–214.
1997. The composite square-mesh panel: a modification to codends for reducing unwanted bycatch and increasing catches of prawns throughout the New South Wales oceanic prawn-trawl fishery. Fish. Bull. 95:653–664.

Broadhurst, M. K., S. J. Kennelly, and S. Eayrs.
1999. Flow-related effects in prawn-trawl codends: potential for increasing the escape of unwanted fish through square-mesh panels. Fish Bull 97(1):1–8.

Fonteyne, R., and R. M'Rabet.
1992. Selectivity experiments on sole with diamond and

square mesh codends in the Belgian coastal beam trawl fishery. Fish. Res. 13:221–233.

Fryer, R. J.
1991. A model of between-haul variation in selection. ICES J. Mar. Sci. 48:281–290.

Karlsen, L., and R. Larsen.
1989. Progress in the selective shrimp trawl development in Norway. *In* C. M. Campbell (ed.), Proceedings of the world symposium on fishing gear and fishing vessels, p. 30–38. Marine Institute, St Johns, Canada.

Kennelly, S. J., and M. K. Broadhurst.
1995. Fishermen and scientists solving bycatch problems: Examples from Australia and possibilities for the northeastern United States. *In* Solving bycatch: considerations for today and tomorrow, p 121–128. Alaska Sea Grant College Program Report 96-03, Univ. Alaska, Fairbanks, AK.

Lochhead, J. H.
1961. Locomotion. *In* T. H. Waterman (ed.), The physiology of the Crustacea, 681 p. Academic Press, New York, NY.

Millar, R. B., and S. J. Walsh.
1992. Analysis of trawl selectivity studies with an application to trouser trawls. Fish. Res. 13:205–220.

Pope, J. A., A. R. Margetts, J. M. Hamley, and E. F. Akyuz.
1975. Manual methods for fish stock assessment. Part III: Selectivity of fishing gear. FAO Fisheries Technical Report 41 (revision 1), 65 p.

Renaud, M., G. Gitschlag, E. Kilma, A. Shan, D. Koi, and J. Nance.
1993. Loss of shrimp by turtle excluder devices (TEDs) in coastal waters of the United Sates, North Carolina to Texas: March 1988–August 1990. Fish. Bull. 91:129–137.

Robertson, J. H. B., and P. A. M. Stewart.
1988. A comparison of size selection of haddock and whiting by square and diamond mesh codends. J. Cons. Int. Explor. Mer 44:148–161.

Robins-Troeger, J. B., R. C. Buckworth, and M. C. L. Dredge.
1995. Development of a trawl efficiency device (TED) for Australian prawn fisheries. II. Field evaluations of the AusTED. Fish. Res. 22:107–117.

Rogers, D. R., B. D. Rogers, J. A. de Silva, and V. L. Wright.
1997. Effectiveness of four industry-developed bycatch reduction devices in Louisiana's inshore waters. Fish. Bull. 95:552–565.

Suuronen, P., and R. B. Millar.
1992. Size selectivity of diamond and square mesh codends in pelagic herring trawls: Only small herring will notice the difference. Can. J. Fish. Aquat. Sci. 49:2104–2117.

Thorsteinsson, G.
1992. The use of square mesh codends in the Icelandic shrimp *(Pandalus borealis)* fishery. Fish. Res. 13:255–266.

Tokai, T., H. Ito, Y. Masaki, and T. Kitahara.
1990. Mesh selectivity curves of a shrimp beam trawl for southern rough shrimp *Trachypenaeus curvirostris* and mantis shrimp *oratosquilla oratoria*. Nippon Suisan Gakkaishi 56:1231–1237.

Tokai, T., and H. Sakaji.
1993. Mesh selectivity of a shrimp beam trawl for tora velvet shrimp *Metapenaeopsis acclivis*, kishi velvet shrimp *Metapenaeopsis dalei* and smoothshell shrimp *Parapenaeopsis tenella*. Bull. Nansei Natl. Fish. Res. Inst. 26:21–30.

Walsh, S.J., R. B. Millar, C. G. Cooper, and W. M. Hickey.
1992. Codend selection in American plaice: diamond versus square mesh. Fish. Res. 13:235–254.

Watson, J. W.
1976. Electrical shrimp trawl catch efficiency for *Penaeus duorarum* and *Penaeus aztecus*. Trans. Am. Soc. 105: 135–148.

Watson, J. W., J. F., Mitchell, and A. K. Shan.
1986. Trawling efficiency device: A new concept for selective shrimp trawling gear. Mar. Fish. Rev. 48(1):1–9.

Wileman, D. A., R. S. T. Ferro, R. Fonteyne, and R. B. Millar.
1996. Manual methods of measuring the selectivity of towed fishing gears. ICES, Copenhagen, 126 p.

Appendix

The plots of deviance residuals (Fig. 7) for both selection curves provided in Figure 6 showed that most of the size classes of prawns above 45-mm carapace length had high deviances. By removing these data from analysis and also the frequencies for the 35- and 36-mm size classes from the composite-square-3 codend, the *P*-values for model goodness-of-fit increased from 0.760 to 0.999 for the composite-square-2 codend (df=25) and from 0.221 to 0.853 for the composite-square-3 codend (df=21) (Table 4). Although this alternative analysis does provide selectivity parameters that are slightly different from those calculated in Table 3, the overall interpretation of the data remains the same.

Table 4

Computed selectivity parameters for prawns (carapace length in mm) from the two composite square-mesh codends and deviance values for logistic curve goodness-of-fit, excluding all entries above 45-mm carapace length for both codends and the 35- and 36-mm size classes from the composite-square-3 codend. Standard errors are given in parentheses. a, b = logistic parameters (Pope et al., 1975). P = split proportion from estimated split model (Millar and Walsh, 1992).

	Composite-square-2 codend		Composite-square-3 codend	
a	−9.556		−13.58	
b	0.330		0.424	
P	0.513		0.573	
		95% confidence limits		95% confidence limits
25% retention (L_{25})	25.59 (0.60)	21.80–29.17	29.46 (0.59)	26.33–32.38
50% retention (L_{50})	28.92 (0.63)	27.73–30.42	32.05 (0.66)	30.90–33.67
75% retention (L_{75})	32.24 (0.92)	28.68–36.64	34.64 (0.96)	31.77–38.67
Selection range (SR)	6.65 (0.92)	4.84–8.45	5.18 (0.81)	3.42–6.95
Deviance	7.91		14.75	
df	25		21	
P–value	0.999		0.853	

Morphometric criteria for estimating sexual maturity in two snappers, *Etelis carbunculus* and *Pristipomoides sieboldii*

Edward E. DeMartini

Boulderson B. Lau

Honolulu Laboratory
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole Street
Honolulu, Hawaii 96822-2396

E-mail address (for E.E. DeMartini): Edward.DeMartini@noaa.gov

Abstract.—A gross measure of reproductive condition (ovary weight adjusted for body size and oocyte volume) is developed and evaluated as an alternative to commonly used gonad indices, for classifying the maturity status of individual ehu (*Etelis carbunculus*) and kalekale (*Pristipomoides sieboldii*), two species of eteline snappers (Lutjanidae) that contribute to the deep-slope handline fishery in Hawaii. Discriminant analysis and logistic regression, based on body length, ovary weight, and oocyte volume, were used to classify fish as either immature or mature. Discriminant analysis correctly classified the maturity of about 98% of both ehu and kalekale, with histological criteria as the standard for comparison. Logistic regression correctly classified maturity of 97% of the ehu and 100% of the kalekale. Misclassification errors increased by 3.75–5% (discriminant analysis) or 0–5% (logistic regression) if oocyte volume was excluded and only body length and ovary weight were used as predictors of maturity.

For kalekale, estimates of lengths at which 50% are sexually mature (L_{50}) were identical (29.0 ±1.8 [SE] cm fork length, FL; r^2=0.92), when maturity was classified histologically or by logistic regression on body, ovary, and oocyte metrics. For ehu, L_{50} estimates were similar (r^2=0.96) for maturity assignments based on histology (27.9 ±2.4 cm FL) and on logistic regression using gross metrics (27.8 ±2.3 cm FL).

We conclude that gross morphometrics can provide adequate proxies for histological evidence when categorizing sexual maturity in asynchronous, multiple-spawning fishes like eteline lutjanids. The potential benefits of using gross metrics for assessing sexual maturity in other serial spawners are briefly discussed.

Manuscript accepted 28 August 1998.
Fish. Bull. 97:449–458 (1999).

Body size at sexual maturity is of fundamental importance in fishery stock assessment (e.g. when calculating a "spawning potential ratio" [SPR, Goodyear, 1993; Somerton and Kobayashi[1]]). In fisheries applications, average size at maturity is usually expressed as the body length at which 50 percent of females are mature (L_{50}), and is typically estimated by fitting a model such as the logistic (Gunderson et al., 1980; O'Brien et al., 1993) to observed percentages of mature fish within several length classes. Estimating percentage mature by size class assumes that individuals can be accurately classified as either immature or mature.

Various methods have been used to classify individual female fish as sexually mature, including gross inspection of ovaries, light microscopic examination and measurement of whole oocytes in fixed tissue samples, histological stains of intraovarian inclusions, and an array of ratios, commonly referred to as "gonad indices" or "gonadosomatic indices" (GSIs) that standardize gonad mass to body size. These methods differ in precision, accuracy, and processing time. Gross inspection of ovaries is quick but highly subjective and often cannot be used to distinguish between immature and spent (resting) mature fish (West, 1990). Light microscopy of whole oocytes can effectively identify the most advanced oocyte mode only if the dynamics of oocyte growth are known for the particular species and may be inaccurate for ovaries that also contain oocytes in intermediate stages of vitellogenesis (West, 1990). Histological staining of tissue samples for detection of cytoplasmic inclusions (yolk, oil globule presence and number) in the most advanced oocytes provides the best evidence of maturation and is the most accurate method, but it is also the most time consuming and expensive (Delahunty and deVlaming, 1980).

Usually only a single method has been used in a given study, although some studies (e.g. Cayre and Laloe, 1986; Hay et al., 1987; Kjesbu, 1991; Olsen and Rulifson, 1992; Ramsay and Witthames, 1996) have at least attempted to confirm maturity classifications with more than one technique. Average size at maturity has usually (e.g. Higham and Nicholson, 1964; DeMartini and Fountain, 1981), but not always (Erickson et al., 1985a; Matsuyama et al., 1987; McQuinn, 1989; Hunter et al., 1992;

[1] Somerton, D. A., and D. R. Kobayashi. 1990. A measure of overfishing and its application on Hawaiian bottomfishes. Honolulu Laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Sci. Cent. Admin. Rep. H-90-10, 18 p.

Render et al., 1995), been identified subjectively if more than one method of classification was used, sometimes with inconsistent results (Trippel and Harvey, 1991). Recently, West (1990) identified microscopic staging coupled with a gonad index as the most objective and quantitative method.

Gonad indices should be used with caution as measures of sexual maturity and require biologically realistic companion analyses (e.g. Koya et al., 1995). A fundamental flaw of ratios, such as gonad indices, is that they either lose or obscure meaningful information in the numerator and denominator of the ratio (Garcia-Berthou and Moreno-Amich, 1993). Gonad indices also are questionably applicable for asynchronous, multiple-spawning fishes (deVlaming et al., 1982). There are two major reasons for this. First, because multiple-spawners ripen and shed numerous batches of eggs, the ovary weight of an individual fish fluctuates cyclically and often greatly during the spawning season. Second, somatic weight often varies independently of ovary weight for individuals. Somatic "condition" (robustness) usually declines monotonically, and sometimes greatly, as somatic energy reserves become progressively depleted over the spawning season, whereas ovary weights cycle high and low as the individual continues to spawn (Delahunty and deVlaming, 1980; deVlaming et al., 1982). Variances in GSIs among mature fish are unavoidably large (e.g. Macer, 1974) because small, ready-to-spawn fish sometimes have higher GSIs than larger fish that have just shed their eggs. Other potential complications include differences in ovarian cycling frequencies (spawning intervals) between small and large females within populations (Hunter and Macewicz, 1985). Thus even refinements of the conventional GSI such as the "relative gonadal index" (RGI) of Erickson et al. (1985b), in which gonadal investment is adjusted for size allometry, can be inappropriate for asynchronous, multiple-spawners if the dynamics of somatic and gonadal condition are unknown. Statistical descriptors of sexual maturity that are more accurate and robust than GSIs need to be developed (Garcia-Berthou and Moreno-Amich, 1993; Winters and Wheeler, 1996; Jons and Miranda, 1997).

Our study has several complementary objectives. First, we evaluate four gross metrics (fish body length and weight, ovary weight, and oocyte size) for describing stages of sexual maturation in two eteline lutjanids (ehu, *Etelis carbunculus*, and kalekale, *Pristipomoides sieboldii)* that contribute to the deep-slope bottom fishery in Hawaii. We examine these four characters because they are readily measured and less costly than the more accurate histological staining of ovarian tissue. We also independently assess stage of sexual maturity for each species based on histology of ovarian tissue samples from specimens collected during peak periods of spawning. In our study, we use discriminant analysis and logistic regression to further classify individual fish as either immature or mature on the basis of gross morphometric and histological criteria. In conclusion, we evaluate the results of gross classifications of maturity for ehu and kalekale by assessing how well L_{50} estimates based on statistical assignments of maturity with gross metrics agree with L_{50} estimates based on histological evidence of maturity.

Materials and methods

Fish collection and shipboard processing

Two types of fish collections were used: hook and line and bottom trawling. For exploitable-sized fish of both species, hydraulic handline gurdies with sizes 28 and 34 Izuo circle hooks (baited with squid strips) were used to fish near bottom at depths of 60–300 m, on insular slopes and submerged banks located between 22–25°N lat. and 160–170°W long. in the Northwestern Hawaiian Islands (NWHI). Specimens were collected in September 1992; during June, July, August, and September 1993; in August 1996, and in July and August 1997 (Table 1). Most line-fishing was conducted during daylight hours (0730–1930) aboard the NOAA ship *Townsend Cromwell*. Additional small kalekale were sampled at 60–65 m off south Molokai, Main Hawaiian Islands, during August 1992 and September 1993. We also examined additional small ehu caught by bottom trawl at 88–97 m near Kure Atoll (NWHI) in early June 1977 (Table 1). All specimens examined were collected during the protracted summer spawning period of eteline snappers in Hawaiian waters (Ralston, 1981; Everson, 1984; Everson et al., 1988). Ehu are thought to be serial spawners (Everson, 1984), and oocyte size distributions within ovaries suggest that Hawaiian populations of both species comprise asynchronous spawners.[2]

Once captured, fish were placed immediately on ice. Within an hour of capture, fork length (FL) to the nearest 0.1 cm and ovary-free body weight (OFBW, in g) was estimated for each fish.

Ovary weight (OW) of each specimen that appeared female was estimated ±0.1 g (if <5g), ±1 g (if 5–100 g) and ±10 g (if >100 g). A tissue plug (1–50 g, de-

[2] 1994. Honolulu Laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Unpubl. data.

Table 1

Summary statistics for ehu (*Etelis carbunculus*) and kalekale (*Pristipomoides sieboldii*) used in analyses. Months were sampled in the years 1992, 1993, 1996, and 1997. FL = fork length; OFBW = ovary-free body weight; OW = ovary weight.

		FL (mm)		OFBW (g)		OW (g)		
Species	Month	Median	Min–Max	Median	Min–Max	Median	Min–Max	*n*
Ehu	Jun–Jul	368	91–551	865	15–2984	10	0.1–136	37
	Aug	356	203–544	826	200–3260	24	0.3–350	80
	Sep	370	270–595	894	351–3615	28	3.0–200	64
	Total	362	91–595	850	15–3615	23	0.1–350	181
Kalekale	Jun–Jul	340	334–390	714	596–1054	40	26–46	5
	Aug	340	156–438	626	51–1400	20	0.1–120	51
	Sep	363	150–412	846	51–1247	17	0.1–39	24
	Total	348	150–438	710	51–1400	20	0.1–120	80

pending on ovary size, and including the ovarian wall) was taken from the central one-third of either the right or left ovary (random choice) and placed in 10% formalin sea-water.

Laboratory processing

Most ovary specimens were processed within 1–2 months after collection. Diameters of 25 of the largest viable oocytes were then measured (random axis, 63× magnification) for each specimen with a dissecting microscope. The median of 25 diameters provides a cost-efficient estimator of average maximum oocyte size for ehu (Lau and DeMartini, 1994).

For each preserved ovary specimen, a subsample of the ovary was dehydrated, imbedded in paraffin, and a minimum of three sections was cut (at 6 µm) and stained with Harris's hematoxylin, followed by eosin counterstain (Hunter and Macewicz, 1985). Slide sections were examined with a compound microscope at 40–500× for the presence and relative quantity of eosinophilic yolk (unyolked oocytes: class 1 of Murphy and Taylor, 1990; partly yolked: classes 2–3; yolked: classes ≥4). If oocytes were yolked, we further noted the presence of postovulatory follicles (POF: class 6), hydrating or hydrated oocytes (HYD: class 7), and oocytes undergoing α or β atresia (class 8: Murphy and Taylor, 1990). Individuals were designated as "immature" if the most advanced oocytes were unyolked or partly yolked without substantial atresia, "ripening mature" if fully yolked but lacking POF or HYD, "resting mature" if a majority of the yolked oocytes were atretic, or "ripe mature" if POFs or HYDs were present. Fish that might in the future have resorbed yolked oocytes without spawning were necessarily classified as mature.

Statistical analyses

We used oocyte volume (OV) to characterize egg size because a volumetric measure was more directly proportional to OW than was a linear measure such as oocyte diameter. OV was calculated as the volume of a sphere, $4/3\ \pi r^3$, where r was one-half of the median diameter of the largest oocytes (Lau and DeMartini, 1994). The sampling distributions of dependent and regressor variables were first examined by using raw and log-transformed data. Log-transformed data were least skewed; logarithms (base 10) were therefore used in all subsequent analyses.

We used analysis of covariance (ANCOVA) to determine if OW was suitable for quantifying maturation state of individual fish after adjusting OW for body size, egg size, or both measures. For each species, the analysis evaluated fish of three ovarian developmental stages (unripe immature, ripening or resting mature, and ripe mature), identified histologically. We were thereby able to evaluate the potentially confounding effects of oocyte development and body size on ovary weight (Erickson et al., 1985b).

We further used two classification techniques (discriminant analysis and logistic regression) to distinguish between mature and immature fish. These two techniques were used because we recognized the general need, in studies such as this, to classify the maturity status of individual fish 1) based on both gross morphometrics and histological criteria and 2) with gross metrics alone, without the added benefit of histological evidence. At a minimum, ovary tissues of some of the fish examined in any study need to be examined histologically as a check on the accuracy of gross classification.

Both logistic regression and discriminant analysis can be used to classify dichotomous states such

as maturity. The latter is often (Efron, 1975), but not always (Prager and Fabrizio, 1990), the more effective technique. However, it is less robust to violations of the assumption of identical covariance matrices. Multivariate normality is also assumed if linear discriminant functions are fitted parametrically (Press and Wilson, 1978), an assumption we avoided in this study (see below).

For combined gross-histological classifications of maturity, we used predictive discriminant analysis (Huberty, 1994) to distinguish between mature (ripe, ripening or resting) and immature fish. Nonparametric discriminant functions were derived by using the uniform-kernel method with Euclidean distances (Huberty, 1994). We used logistic regression (Hosmer and Lemeshow, 1989) to evaluate whether maturity classifications based on histology could be predicted by the relationships among body size, OW, and OV. Logistic regression coefficients were estimated by maximum likelihood methods. Using each technique, we evaluated the full (three-variable) model first, then a two-variable model without OV. Because sample sizes were small for each species, all sample fish of each species were evaluated histologically.

Once all individuals had been assigned to maturity classes based on histological and gross morphometric criteria, we assigned specimens to 2-cm length classes and calculated the percentage mature for each length class using each set of criteria. Percent maturity (0–100%) was then related to length class by using nonlinear regression weighted by the square root of the numbers of fish in each length class. The logistic model,

$$P_x = 100 / \left(1 + e^{-(a+bFL)}\right),$$

where P_x = percentage mature in each length class;
a and b = fitted parameters; and
L_{50} = $(-a/b)$, was fitted to the data by using maximum likelihood.

Data were analyzed using STATISTIX (v. 4.1; Analytical Software, 1994: logistic regression) and SAS (v. 6.03; SAS Institute, Inc., 1988: PROC REG, GLM, and DISCRIM).

Results

Body size interrelations

After log-transformation, the influences of body length (FL) and ovary-free body weight (OFBW) on ovary weight (OW) were virtually identical; hence, FL (the easier variable to measure) only is reported in Table 2 and used in all subsequent analyses. OFBW was significantly related to FL for each species (ehu: $\log OFBW = -1.720 + 2.971 \log FL$, $r^2=0.979$, $n=172$, $P<0.001$; kalekale: $\log OFBW = -1.785 + 3.010 \log FL$, $r^2=0.966$, $n=75$, $P<0.001$).

Effect of ovarian stage on relation of ovary weight to body length

The OW-to-body length relation marginally differed with ovarian developmental stage for ehu and kalekale (FL × stage interaction in ANCOVA: $F_{2,175}=3.19$ and $F_{2,74}=2.69$, $P=0.04$ and 0.06, respectively; reject H_0: slopes equal). Thus, ovary weights could not be adjusted by body lengths and subsequently used to distinguish among maturation states for either species. Body length was a poor predictor of ovary weight for both ehu and kalekale ($r^2=0.58$ and 0.60, respectively; Table 2).

Effect of egg size

FL and OV together, however, accounted for 91% (ehu) and 82.5% (kalekale) of the variation in OW (Table 2). Colinearity between FL and OV (or OFBW and OV) was unimportant. For example, FL explained only 12% of the variation in OV for ehu.

Histological evidence of maturity

Most specimens of ehu and kalekale were readily classified as either immature or mature according to histological criteria. Kalekale included fish that were immature, ripening mature, and ripe mature (none were resting mature). Unlike kalekale, a minority of the large (>40 cm FL) ehu were resting mature, with ovaries undergoing substantial atresia. The ovaries of kalekale usually contained HYD oocytes if POFs were present (19 of 21 cases). Ehu included specimens with HYD oocytes (7 cases) or POFs (98 cases), but POFs were not observed if HYDs were present (0 of 7 cases). Ehu and kalekale clearly differed in the co-occurrence of HYD oocytes and POFs (Fisher exact test; $P<0.001$), suggesting that the average spawning intervals of individual females probably differ between these two species.

Statistical classifications of maturity

For both species, maturity classifications based on discriminant analysis of the three gross metrics (body length, ovary weight, and oocyte volume) generally agreed (≈98% correct) with those where histological criteria were used (Table 3). Maturity classes determined by histology also were accurately predicted

Table 2

Multiple regression models describing the interrelations of ovary weight (OW), fork length (FL), and oocyte volume (OV) for two species of eteline lutjanids in Hawaii (ehu, *Etelis carbunculus*; kalekale, *Pristipomoides sieboldii*). Mean square errors (MSE) and standard errors of estimates (SE) are noted, with coefficients and standard errors (SE) of model parameters expressed as base 10 logarithms. All regressions are significant, as are the intercepts (all $P<0.001$).

	Model				Coefficient			SE			
Species	$Y = f(X_1+X_2+X_1X_2)$	R^2	n	MSE	b_1	b_2	b_{12}	SE_{b1}	SE_{b2}	SE_{b12}	Intercept
Ehu	$OW = f(FL)$	0.579	172	0.102	4.541	—	—	0.297	—	—	–5.839
	$OW = f(FL + OV)$	0.911	172	0.022	3.284	0.457	—	0.146	0.018	—	–5.508
	$OW = f(FL + OV + FL \times OV)$	0.917	172	0.020	1.077	–.501	0.627	0.646	0.274	0.179	–2.149
Kalekale	$OW = f(FL)$	0.596	75	0.111	7.007	—	—	0.676	—	—	–9.579
	$OW = f(FL + OV)$	0.825	75	0.049	3.877	0.376	—	0.551	0.039	—	–6.297
	$OW = f(FL + OV + FL \times OV)$	0.826	75	0.049	4.424	0.583	–.139	2.308	0.849	0.569	–7.108

Table 3

Summary results of discriminant analysis evaluating the relations among fork length (FL), ovary weight (OW), plus oocyte volume (OV), for ehu (*Etelis carbunculus*) and kalekale (*Pristipomoides sieboldii*). Analogous summary results using FL and OW only. Imm = immature; Mat = mature.

Species	No. classified by histology as	No. classified by analysis as: Imm	Mat	Total	% Error
FL, OW, plus *OV*					
Ehu	Imm	33	0	33	0.00
	Mat	3	145	148	2.03
	Total	36	145	181	1.66
Kalekale	Imm	15	0	15	0.00
	Mat	1	64	65	1.54
	Total	16	64	80	1.25
FL and *OW*					
Ehu	Imm	33	0	33	0.00
	Mat	12	136	148	8.11
	Total	45	136	181	6.63
Kalekale	Imm	14	1	15	6.67
	Mat	3	62	65	4.62
	Total	17	63	80	5.00

(ehu: 97%, kalekale: 100%) by logistic regression using FL, OW, and OV as regressor variables (Table 4). Misclassification errors increased by 3.75–5% (discriminant analysis; Table 3) or 0–5% (logistic regression; Table 4) if oocyte volume was excluded as a predictor of maturity.

Table 4

Summary statistics for logistic regressions used to classify maturity (immature, mature) of ehu (*Etelis carbunculus*; n=181) and kalekale (*Pristipomoides sieboldii*; n=80). Histological maturity was regressed on log-transformations of three gross metrics (fork length, FL; ovary weight, OW; plus egg volume, OV), and FL and OW only. Intercepts and higher-order terms were tested for each model and species, but are unspecified if insignificant.

		Coefficient		
Species	Regressor	Estimate	SE	Prob
Three-variable model				
Ehu	*FL*			ns
	OW	–13.10	6.82	0.055
	OV	–2.64	0.76	0.001
	$OW \times OV$	8.03	2.58	0.002
Total df: 178				
Overall percentage error: 2.8%				
Kalekale	FL			ns
	OW	–309.4	125.3	0.014
	OV	–9.55	5.26	0.069
	$OW \times OV$	125.2	47.2	0.008
Total df: 77				
Overall percentage error: 0%				
Two–variable model				
Ehu	*FL*	–6.08	1.46	<0.001
	OW	12.29	2.75	<0.001
Total df: 179				
Overall percentage error: 2.8%				
Kalekale	FL	–1.74	0.61	0.004
	OW	5.64	1.37	<0.001
Total df: 78				
Overall percentage error: 5.0%				

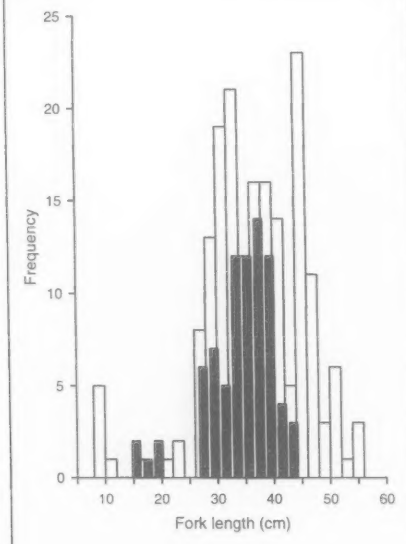


Figure 1

Length-frequency (FL, cm) histograms of ehu, *Etelis carbunculus* (hollow bars, n=181), and kalekale, *Pristipomoides sieboldii* (solid bars, n=80).

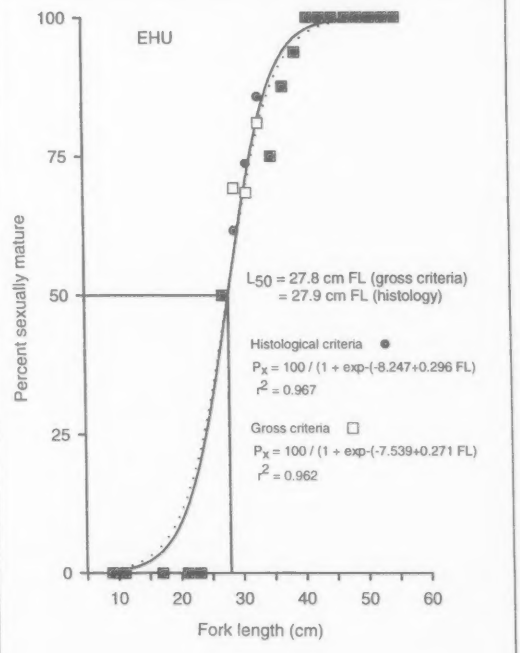


Figure 2

Scatterplots of mean percentage maturity by 2-cm length class, for ehu, *Etelis carbunculus*. Solid circles and solid line represent the observed values and fitted curve based on histological criteria of maturity; hollow squares and dotted line represent the values and curve based on maturity classified by logistic regression on fork length, ovary weight, and oocyte volume. The logistic curves were fitted by nonlinear regression with each class mean weighted by the square root of its count (see Fig. 1).

Size at sexual maturity

For each species, the length-frequency distribution comprised relatively few individuals <30 cm FL (Fig. 1). Hence, our size-at-maturity characterizations might have been affected by the scarcity of immature specimens.

Ehu On average, ehu in Hawaiian waters mature at an estimated 27.9 cm FL (95% CI=25.5–30.3 cm) according to histological criteria or 27.8 (25.5–30.1) cm FL based on logistic regression according to gross criteria (r^2=0.967 and 0.962, respectively; Fig. 2). The precision of these L_{50} estimates is reasonable despite the discontinuous lower tail of the size-frequency distribution. Our L_{50} estimates for ehu provide an adequate objective basis for evaluating gross and histological classifications; however, they should be considered only as preliminary estimates of size at maturity.

Kalekale A body length-maturity pattern also was strongly evident for this species. Whether based on histological evidence or logistic regression with gross metrics, size at maturity was well described by the logistic model (r^2=0.920; Fig. 3). Kalekale in Hawaiian waters mature at 29.0 (95% CI=27.2–30.8) cm FL, according to histological and gross criteria (Fig. 3).

Discussion

Gross metric criteria

For both ehu and kalekale, the proportional weight of ovaries increased allometrically with body length (coefficients of b_1 >> 3; Table 2), which is typical for asynchronous multiple-spawners (Reiss, 1987). Our results further confirm that gonad indices are unsuitable for identifying maturity stages in asynchronous multiple-spawners because the rate at which ovary weight increases with body size differs among fish of different maturation stages (deVlaming et al., 1982; Erickson et al. 1985b). Body size, ovary size,

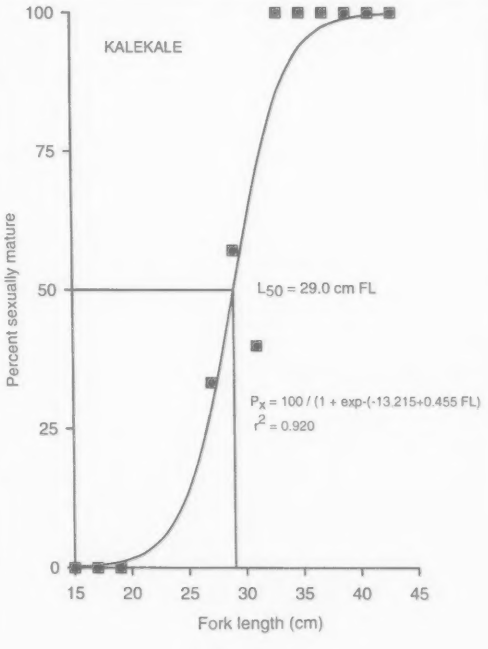


Figure 3

Scatterplots of mean percentage maturity by 2-cm length class, for kalekale, *Pristipomoides sieboldii*. Solid circles inside hollow squares and solid line represent the congruent observed values and fitted curve based on histological criteria of maturity and on maturity classified by logistic regression on fork length, ovary weight, and oocyte volume. The logistic curve was fitted by nonlinear regression with each class mean weighted by the square root of its count (see Fig. 1).

and oocyte size can be used to classify maturity directly by using either discriminant analysis or logistic regression, however. Logistic regression may be more applicable in most studies because of its less stringent assumptions (Press and Wilson, 1978). We recommend using body length for these types of analyses because length data are easier to obtain than weight data.

Relative merits of gross and histological evidence

Histological inspection of stained ovary sections provides the most accurate assessment of sexual maturity, but at the greatest cost. Gross morphometrics can be used to characterize maturity at a greatly reduced cost, but are less accurate predictors. The benefit of a gross morphometric proxy depends on whether the loss in accuracy is outweighed by the cost savings. In our study, assignments of sexual maturity based on discriminant analysis or logistic regression with body length or weight, ovary weight, and oocyte volume were accurate (97–100% correct classification) for ehu and kalekale. Analogous maturity assignments based on only body size and ovary weight (omitting oocyte volume) were less accurate (93–97% correct), indicating a small but real contribution of the egg size variable. Whether the benefit of including an egg size variable merits the cost of its measurement will vary with the particular study. The egg size variable likely had no effect in the logistic regression model for ehu because our specimens included resting mature fish (undergoing oocyte atresia) with small viable oocytes. Two of the three ehu (32.5, 36.2 cm FL) that were misclassified as immature by discriminant analysis with body length, ovary weight, and egg size were resting mature fish. Our ehu data perhaps illustrate discrepancies between gross and histological classifications that might arise when histological criteria for maturity include evidence such as atresia that is unrelated to oocyte mass. Gross criteria likely are most accurate in cases in which samples are collected during peak spawning periods when most fish are actively spawning. Histological criteria may be less than 100% accurate for cases (such as ehu, this study) in which some adolescent fish may resorb yolked oocytes before first spawning (De Veen, 1970; Ramsay and Witthames, 1996). The ability to determine maturity status with reasonable accuracy with only gross metrics in this study nonetheless suggests that such methods warrant further application and evaluation.

Size at sexual maturity

Ehu Our current best estimate of L_{50} for ehu in Hawaiian waters (≈28 cm FL) must be considered preliminary because data for small immature fish are relatively few. Everson (1984), in his pilot evaluation of size at maturity for ehu from Hawaiian waters, also had few small specimens: only 2/185 fish collected during the May–September spawning seasons of 1977–81 were <30 cm FL. Prior to the estimates provided in the present study, those provided by Everson (1984) were the only size-at-maturity estimates available for use in managing ehu in Hawaii (Kobayashi[3]).

Our paucity of specimens <25 cm FL might have reflected hook-size selectivity (Ralston, 1990). How-

[3] Kobayashi, D. R. 1993. Effects of increasing the minimum size limit or imposing fishing closures on three species of Hawaiian deepwater snappers. Honolulu Laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Admin. Rep. H-93-01, 18 p.

ever, ehu have relatively large mouths, take baited hooks aggressively (Ralston, 1990), and small-mouthed kalekale were well-represented in our catches. We therefore should have caught small, immature ehu had they been abundant where we fished. Alternatively, juvenile ehu might occupy different bottom depths, as evident for several species of eteline snappers elsewhere (Ralston and Williams, 1988; Parrish, 1989). If so, juvenile ehu inhabit considerably different depths than do larger fish because we fished at depths that were much shallower and deeper than the typical (175–225 m) depths at which adult ehu occur in Hawaiian waters. It is more likely that juvenile ehu occur in different, perhaps lower-relief microhabitats at or near depths at which larger conspecifics are fished in Hawaii (Clarke, 1972; Struhsaker, 1973).

Our estimate of L_{50} for ehu approximates the norm for deepwater lutjanids: 28 cm FL is equivalent to 43% of its reported maximum body length in Hawaiian waters of 65 cm FL (Everson, 1984). On average, deepwater insular snappers mature at about 50% maximum body length, although values can range considerably lower and higher among species (Grimes, 1987).

Researchers must not apply size-at-maturity estimates to other populations of the same species for which somatic condition (Ralston, 1988) or size-specific gonadal allocation might differ, because to do so could result in erroneous estimates of size at maturity. For example, body size at maturity estimated for ehu in this report is applicable only to fish in the Hawaiian archipelago. It is almost certain that body size at sexual maturity differs among Pacific regions, given the great geographic variations in average and maximum body sizes and growth rates of ehu (Smith, 1992; Moffitt, 1993). The L_{50} value for ehu in the South Pacific (Vanuatu), where the species attains maximum body lengths of 120 cm FL, is likely greater than that for ehu in Hawaii. Conversely, our value may be an overestimate in the Marianas, where ehu apparently attain maximum body lengths of less than half those at Vanuatu (Smith and Kostlan, 1991). Improved estimates of L_{50}, based on more data for smaller fish, are needed for ehu in Hawaii. Better age and growth estimates also are needed for ehu in Hawaii and elsewhere because of uncertainties in present size-at-age and growth-rate estimates for the species (Smith and Kostlan, 1991; Kobayashi[3]).

Kalekale We provide the first direct estimates of size at maturity of this species. In age and growth studies of kalekale from the Marianas (Ralston and Williams, 1988) and Hawaiian Islands (Williams and Smith, 1997), deceleration in somatic growth (which should reflect gonadal maturation) occurred at lengths of 25–30 cm FL, consistent with our estimated size at maturity for this species. An L_{50} of 29 cm FL is about 53% of its estimated maximum length in Hawaii (55 cm, as 105% of L_{∞}=52.5 cm FL; Fig. 4 in Williams and Smith, 1997), also approximating the 50% norm for deepwater insular lutjanids (Grimes, 1987).

Conclusions

We believe that gross morphometric measures, such as body size, ovary weight, and egg size, can provide adequate proxies for microscopic histological evidence of sexual maturity in asynchronous multiple-spawners like eteline lutjanids in Hawaii. Applicability may vary among species and may relate to the reproductive dynamics of females, both individually and collectively, within spawning populations. We further suggest that these types of measures can be realistically combined to assess sexual maturity using logistic regression or discriminant analysis for other species of temperate and tropical marine fishes.

Acknowledgments

We thank all those who assisted in specimen collection aboard the *Townsend Cromwell*. Eric Yamanoha (Pathology Department, Queen's Hospital, Honolulu) diligently supervised the histological work. We also thank C. Boggs, T. Clarke, D. Ellis, D. Kobayashi, J. Parrish, J. Polovina, D. Somerton, and two anonymous reviewers for constructive reviews of manuscript drafts, and A. Taylor for suggesting logistic regression as an alternative to discriminant analysis. BBL gratefully acknowledges the support of a NOAA Junior Fellowship (1991–95) at the Honolulu Laboratory of the NMFS, Southwest Fisheries Science Center.

Literature cited

Analytical Software
1994. STATISTIX user's manual, version 4.1. Analytical Software, Tallahassee, FL, 329 p.

Cayre, P., and F. Laloe
1986. Review of the gonad index (GI) and an introduction to the concept of its "critical value": application to the skipjack tuna *Katsuwonus pelamis* in the Atlantic Ocean. Mar. Biol. 90:345–351.

Clarke, T. A.
1972. Collections and submarine observations of deep benthic fishes and decapod crustacea in Hawaii. Pac. Sci. 26:310–317.

Delahunty, G., and V. L. deVlaming
1980. Seasonal relationships of ovary weight, liver weight and fat stores with body weight in the goldfish (*Carassius auratus* L.). J. Fish Biol. 16:5–13.

DeMartini, E. E., and R. K. Fountain
1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus:* attributes representative of serial spawning fishes. Fish. Bull. 79:547–560.

deVlaming, V., G. Grossman, and F. Chapman
1982. On the use of the Gonosomatic Index. Comp. Biochem. Physiol. 73A:31–39.

De Veen, J. F.
1970. On some aspects of maturation in the common sole *Solea solea* (L.). Ber. Dtsch. Wiss. Komm. Meeresforsch. 21:78–91.

Efron, B.
1975. The efficiency of logistic regression compared to normal discriminant analysis. J. Am. Stat. Assoc. 70:892–898.

Erickson, D. L., M. J. Harris, and G. D. Grossman
1985a. Ovarian cycling of tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean, from the South Atlantic Bight, U.S.A. J. Fish Biol. 27:1131–1146.

Erickson, D. L., J. E. Hightower, and G. D. Grossman
1985b. The relative gonadal index: an alternative index for quantification of reproductive condition. Comp. Biochem. Physiol. 81A:117–120.

Everson, A. R.
1984. Spawning and maturation of the ehu, *Etelis carbunculus*, in the Northwestern Hawaiian Islands. Proc. Res. Inves. NWHI 2:128–148.

Everson, A. R., H. A. Williams, and B. M. Ito
1988. Maturation and reproduction in two Hawaiian eteline snappers, uku, *Aprion virescens*, and onaga, *Etelis coruscans*. Fish. Bull. 87:877–888.

Garcia-Berthou, E., and R. Moreno-Amich
1993. Multivariate analysis of covariance in morphometric studies of the reproductive cycle. Can. J. Fish. Aquat. Sci. 50:1394–1399.

Goodyear, C. P.
1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. *In* S. J. Smith, J. J. Hunt, and D. Rivard (eds.), Risk evaluation and biological reference points for fisheries management, p. 67–81. Can. Spec. Publ. Fish. Aquat. Sci. 120.

Grimes, C. B.
1987. Reproductive biology of the Lutjanidae: a review. *In* J. J. Polovina and S. Ralston (eds.), Tropical snappers and groupers: biology and fisheries management, p. 239–294. Westview Press, Boulder, CO.

Gunderson, D. R., P. Callahan, and B. Goiney
1980. Maturation and fecundity of four species of *Sebastes*. Mar. Fish. Rev. 42(3-4):74–79.

Hay, D. E., D. N. Outram, B. A. McKeown, and M. Hurlburt
1987. Ovarian development and oocyte diameter as maturation criteria in Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 44:1496–1502.

Higham, J. R., and W. R. Nicholson
1964. Sexual maturation and spawning of Atlantic menhaden. Fish. Bull. 63:255–271.

Hosmer, D. W., and S. Lemeshow
1989. Applied logistic regression. John Wiley & Sons, Inc., New York, NY, 307 p.

Huberty, C. J.
1994. Applied discriminant analysis. John Wiley & Sons, Inc., New York, NY, 466 p.

Hunter, J. R., and B. J. Macewicz
1985. Measurement of spawning frequency in multiple spawning fishes. *In* R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, p. 79–94. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

Hunter, J. R., B. J. Macewicz, N. C-h. Lo, and C. A. Kimbrell
1992. Fecundity, spawning, and maturity of female Dover sole *Microstomus pacificus*, with an evaluation of assumptions and precision. Fish. Bull. 90:101–128.

Jons, G. D., and L. E. Miranda
1997. Ovarian weight as an index of fecundity, maturity, and spawning periodicity. J. Fish Biol. 50:150–156.

Kjesbu, O. S.
1991. A simple method for determining the maturity stages of Northeast Arctic cod (*Gadus morhua* L.) by *in vitro* examination of oocytes. Sarsia 75:335–338.

Koya, Y., T. Hamatsu, and T. Matsubara
1995. Annual reproductive cycle and spawning characteristics of the female Kichiji rockfish *Sebastolobus macrochir*. Fisheries Sci. 61:203–208.

Lau, B. B., and E. E. DeMartini
1994. An evaluation of oocyte size in multiple regressions predicting gonad weight from body weight: a test using Hawaiian ehu, *Etelis carbunculus*. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFSC-212, 17 p.

Macer, C. T.
1974. The reproductive biology of the horse mackerel (*Trachurus trachurus* (L.) in the North Sea and English Channel. J. Fish Biol. 6:415–438.

Matsuyama, M., S. Matsuura, Y. Ouchi, and T. Hidaka
1987. Maturity classification and group maturity of the red sea bream *Pagrus major*. I. Female maturity. Mar. Biol. 96:163–168.

McQuinn, I. H.
1989. Identification of spring and autumn spawning herring (*Clupea harengus harengus*) using maturity stages assigned from a Gonadosomatic Index model. Can. J. Fish. Aquat. Sci. 46:969–980.

Moffitt, R. B.
1993. Deepwater demersal fish. *In* A. Wright, and L. Hill (eds.), Nearshore marine resources of the South Pacific: information for fisheries development and management, p. 73–95. Inst. Pacific Studies, Suva, Fiji. Forum Fisheries Agency, Honiara. International Centre for Ocean Development, Canada, 710 p.

Murphy, M. D., and R. G. Taylor
1990. Reproduction, growth, and mortality of red drum *Sciaenops ocellatus* in Florida waters Fish. Bull. 88:531–542.

O'Brien, L., J. Burnett, and R. K. Mayo
1993. Maturation of nineteen species of finfish off the northeast coast of the United States, 1985–1990. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 113, 66 p.

Olsen, E. J., and R. A. Rulifson
1992. Maturation and fecundity of Roanoke River-Albemarle Sound striped bass. Trans. Am. Fish. Soc. 121:524–537.

Parrish, F. A.
1989. Identification of habitat of juvenile snappers in Hawaii. Fish. Bull. 87:1001–1005.

Prager, M. H., and M. C. Fabrizio
1990. Comparison of logistic regression and discriminant analyses for stock identification of anadromous fish, with application to striped bass (*Morone saxatilis*) and Ameri-

can shad (*Alosa sapidissima*). Can. J. Fish. Aquat. Sci. 43:1570–1577.

Press, S. J., and S. Wilson
1978. Choosing between logistic regression and discriminant analysis. J. Am. Stat. Assoc. 73:699–705.

Ralston, S.
1981. A study of the Hawaiian deepsea handline fishery with special reference to the population dynamics of opakapaka, *Pristipomoides filamentosus* (Pisces: Lutjanidae). Ph.D. diss., Univ. Washington, Seattle, WA, 204 p.

Ralston, S.
1988. Length-weight regressions and condition indices of lutjanids and other deep slope fishes from the Mariana Archipelago. Micronesica 21:189–197.

Ralston, S.
1990. Size selection of snappers (Lutjanidae) by hook and line gear. Can. J. Fish. Aquat. Sci. 47:696–700.

Ralston, S. V., and H. A. Williams
1988. Depth distributions, growth, and mortality of deep slope fishes from the Mariana Archipelago. U.S. Dep. Commer, NOAA Tech. Memo. NMFS-SWFC-113, 47 p.

Ramsay, K., and P. Witthames
1996. Using oocyte size to assess ovarian development in *Solea solea* (L.). J. Sea Res. 36:275–283.

Reiss, M. J.
1987. The intraspecific relationship of parental investment to female body weight. Functional Ecol. 1:105–107.

Render, J. H., B. A. Thompson, and R. L. Allen
1995. Reproductive development of striped mullet in Louisiana estuarine waters with notes on the applicability of reproductive assessment methods for isochronal species. Trans. Am. Fish. Soc. 124:26–36.

Smith, M. K.
1992. Regional differences in otolith morphology of the deep slope red snapper *Etelis carbunculus*. Can. J. Fish. Aquat. Sci. 49:795–804.

Smith, M. K., and E. Kostlan
1991. Estimates of age and growth of ehu (*Etelis carbunculus*) in four regions of the Pacific from the density of daily increments in otoliths. Fish. Bull. 89:461–472.

SAS Institute, Inc.
1988. SAS/STAT guide for personal computers, 6th ed. SAS Inst., Cary, NC, 1028 p.

Struhsaker, P.
1973. A contribution to the systematics and ecology of Hawaiian bathyal fishes. Ph.D. diss., Univ. Hawaii, Honolulu, HI, 482 p.

Trippel, E. A., and H. H. Harvey
1991. Comparison of methods used to estimate age and length of fishes at sexual maturity using populations of white sucker (*Catostomus commersoni*). Can. J. Fish. Aquat. Sci. 48:1446–1459.

West, G.
1990. Methods of assessing ovarian development in fishes: a review. Aust. J. Mar. Freshwater Res. 41:199–222.

Williams, H. A., and M. K. Smith
1997. Growth rates of four Hawaiian deep slope fishes: a comparison of methods for estimating age and growth from otolith microincrement widths. Can. J. Fish. Aquat. Sci. 54:126–136.

Winters, G. H., and J. P. Wheeler
1996. Environmental and phenotypic factors affecting the reproductive cycle of Atlantic herring. ICES J. Mar. Sci. 53:73–88.

Age and growth of cobia, *Rachycentron canadum*, from the northeastern Gulf of Mexico

James S. Franks
Gulf Coast Research Laboratory
Institute of Marine Sciences
University of Southern Mississippi
P.O. Box 7000
Ocean Springs, Mississippi 39566-7000
E-mail address: jfranks@seahorse.ims.usm.edu

James R. Warren
Gulf Coast Research Laboratory
Institute of Marine Sciences
University of Southern Mississippi
P.O. Box 7000
Ocean Springs, Mississippi 39566-7000

Michael V. Buchanan
Mississippi Department of Marine Resources
1141 Bayview Avenue, Suite 101
Biloxi, Mississippi 39530

Abstract.–We examined 1005 cobia, *Rachycentron canadum*, from recreational catches in the northeastern Gulf of Mexico from 1987 to 1995. Specimens ranged from 325 to 1651 mm fork length (FL); females had a mean FL of 1050 mm (n=730) and were significantly larger than males that had a mean FL of 952 mm (n=275). The overall male to female ratio was 1:2.7. Ages of 565 cobia were estimated from thin-sectioned otoliths (sagittae). Marginal-increment analysis of sagittal otoliths showed a single annual minimum during June. Male cobia (n=170; 525–1330 mm FL) ranged from age 0 to 9, and females (n=395; 493–1651 mm FL) ranged from age 0 to 11. The relationship of observed fork length and age was described by the von Bertalanffy growth equation for males $FL_t = 1171(1-\exp[-0.432(t+1.150)])$ and for females $FL_t = 1555(1-\exp[-0.272(t+1.254)])$. Growth in length for both sexes was relatively fast through age 2, after which growth slowed gradually. Estimates of the von Bertalanffy growth equation parameters L_∞ and K were significantly different for males and females, whereas estimates for t_0 were not significantly different. Sagittal otolith weight was a good predictor of age. The instantaneous rate of total mortality (Z) estimated by catch curve analysis for fully recruited ages 4–8 was 0.75.

Manuscript accepted 28 August 1998.
Fish. Bull. 97:459–471 (1999).

Cobia, *Rachycentron canadum*, are large, migratory, coastal pelagic fish of the monotypic family Rachycentridae and are distributed worldwide in tropical and subtropical seas, except for the eastern Pacific (Briggs, 1960; Shaffer and Nakamura, 1989). In the western Atlantic Ocean, cobia occur from Massachusetts and Bermuda to Argentina (Briggs, 1958) but are most common along the U.S. south Atlantic coast and in the northern Gulf of Mexico (Shaffer and Nakamura, 1989). In the Gulf of Mexico (Gulf), where they range from Key West, Florida, along the entire coast to Campeche, Mexico (Dawson, 1971), *R. canadum* is a highly-prized recreational species and is caught incidentally in several commercial fisheries (Shaffer and Nakamura, 1989). Cobia landings, recreational and commercial combined, from the Gulf and Atlantic averaged one million kilograms (kg) per year during a recent 12-year period (1984–95), of which 87% was recreational catch.[1] The majority of recreational landings of cobia in the United States are from the Gulf (Shaffer and Nakamura, 1989) and averaged 0.5 million kg for years 1984-95.[1] Recreational and commercial cobia regulations enacted in U.S. waters presently consist of a minimum size of 838 mm fork length (33 inches) and daily bag and possession limits of two fish per person.[2]

In the eastern Gulf, cobia typically migrate from their wintering grounds off south Florida into

[1] Gulf of Mexico and South Atlantic Fishery Management Councils. 1996. Report of the mackerel stock assessment panel meeting, April 15–18, 1996, Tampa, FL. Gulf Mex. Fish. Manage. Counc., Tampa, FL, and South Atlan. Fish. Manage. Counc., Charleston, SC.

[2] Gulf of Mexico and South Atlantic Fishery Management Councils. 1990. Amendment No. 5, fishery management plan for the coastal migratory pelagic resources (mackerels); environmental assessment and supplemental regulatory impact review. Gulf Mex. Fish. Manage. Counc., Tampa, FL, and South Atlantic Fish. Manage. Counc., Charleston, SC.

northeastern Gulf waters during early spring. They occur off northwest Florida, Alabama, Mississippi and southeast Louisiana from late-March through October, and return to their wintering grounds in the fall (Franks et al., 1991; Biesiot et al., 1994). Howse et al. (1992) reported that some cobia overwinter in the northern Gulf at depths of 100–125 m.

Information on the life history of cobia from the Gulf and U. S. Atlantic coast is limited. Most studies from the Gulf have addressed the occurrence and distribution of early life stages (Dawson, 1971; Ditty and Shaw, 1992), reproductive biology (Biesiot et al., 1994; Lotz et al., 1996; Thompson et al.[3]), and feeding (Knapp, 1949, 1951; Miles, 1949; Franks et al., 1996; Meyer and Franks, 1996). Hassler and Rainville (1975) collected cobia eggs from the Gulf Stream off North Carolina, successfully hatched most of them, and reared the larvae through juvenile stages. Mitochondrial DNA analyses of cobia from the northeastern Gulf and U.S. Atlantic coast suggest that cobia from those two areas are a unit stock (Hrincevich, 1993). Biesiot et al. (1994) induced spawning in ripe, wild-caught females from the northeastern Gulf, Howse et al. (1975, 1992) described diseased heart tissues and ubiquitous perivenous smooth muscle cords in viscera of cobia from northern Gulf waters, and Franks (1995) reported on an anomalous specimen collected off Mississippi. Only a limited amount of information is available on the age and growth of cobia from the Gulf (Thompson et al.[3]; Franks and McBee[4]) or the U.S. Atlantic coast (Joseph et al., 1964; Richards 1967, 1977; Smith, 1995). The objectives of our study were to evaluate sectioned sagittal otoliths for ageing cobia from the northeastern Gulf, construct age-length keys, derive theoretical growth parameters, and obtain length-weight relationships.

Materials and methods

We sampled cobia caught by recreational hook-and-line gear in the northeastern Gulf during 1987–95. Cobia were sampled at the dock and at fishing tournaments. Fish were caught in an area located north of lat. 29°N and between long. 85°20'W and long. 89'W (Fig. 1) in waters that ranged from 2 to 200 m deep. Additional specimens from northwest Florida were provided by the National Marine Fisheries Service (NMFS), and marine enforcement personnel with the NMFS and the Mississippi Department of Marine Resources provided confiscated undersized specimens. Owing to the migratory nature of cobia, abundance varied seasonally. Most fish that we examined

[3] Thompson, B. A., C. A. Wilson, J. H. Render, and M. Beasley. 1991. Age, growth and reproductive biology of greater amberjack and cobia from Louisiana waters. Year 1. Rep. to U. S. Dep. Commer., NOAA, NMFS, Coop. Agreement NA90AA-H-MF089, Marine Fisheries Initiative (MARFIN) Prog., Coastal Fish. Inst., Louisiana St. Univ., Baton Rouge, 55 p.

[4] Franks, J. S., and T. M. McBee. 1991. Age and growth. *In* J. S. Franks, T. D. McIlwain, R. M. Overstreet, J. T. McBee, J. M. Lotz, and G. Meyer, Investigations of the cobia (*Rachycentron canadum*) in Mississippi marine waters and adjacent Gulf waters. Gulf Coast Res. Lab., Ocean Springs, MS 39564-7000. Final Rep. to Miss. Dep. Wildl., Fish. and Parks/Bur. Mar. Res. (Dep. Mar. Res.), 1141 Bayview Ave., Biloxi, MS 39531 and U. S. Fish Wildl. Serv., Atlanta, GA 30345, Proj. No. F-91, p. 1-1 to 1-60.

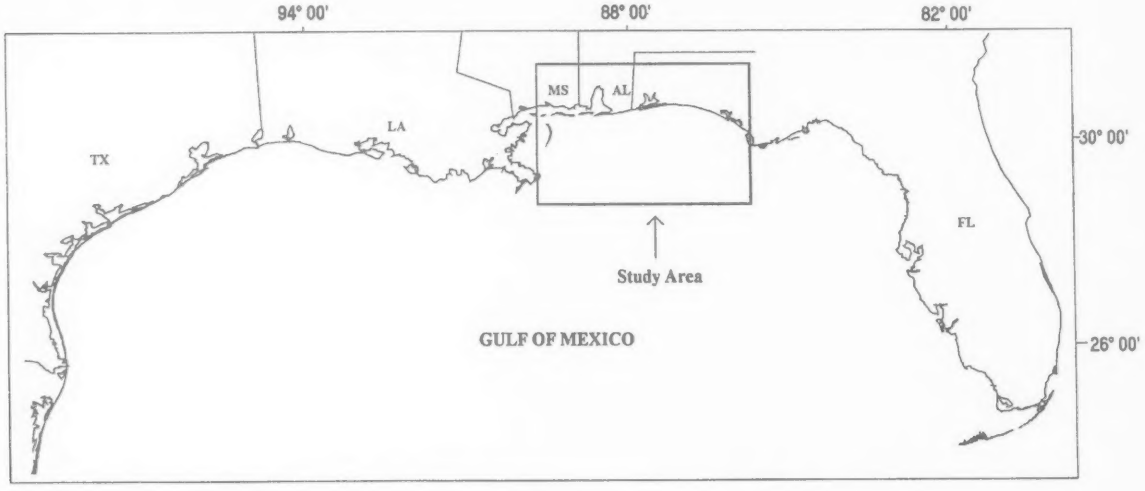


Figure 1

Map of the Gulf of Mexico showing the northeastern Gulf study area where cobia, *Rachycentron canadum*, were caught by hook-and-line gear, 1987–95.

were collected from April through July (n=787); peak samples were taken in May (n=349). Fewer fish were collected in August (n=49) and September through November (n=157). No samples were collected in December, and only 12 samples were collected from January through March.

For most fish, the date and location of catch were recorded along with fork length (FL, mm), total length (TL, mm), and total weight (TW, nearest 0.1 pound converted to kilograms), although some fish had been gutted. All lengths reported are FL. The sex of most fish was also recorded, including that of several young-of-the-year (YOY). Sex-specific length-weight regressions were calculated by linear regression of $\log_{10}$-transformed data, and the slopes and elevations of the regressions were compared by using analysis of covariance (Snedecor and Cochran, 1967). Relationships of fork length to total length were calculated by using the generalized linear regression model: $FL=a+bTL$.

Sagittal otoliths were removed from most specimens, then cleaned with distilled water, air dried, and stored dry in labeled vials. Cobia sagittae are small and fragile. They are elongate, laterally compressed structures, with a rounded posterior, a pointed rostrum, and a smaller, pointed antirostrum (Fig. 2). The distal surface is concave, and a wide, curved sulcus traverses the proximal surface longitudinally. Initially, we randomly selected ten sagittal otolith pairs (fish FL=700–1613 mm) to determine the number of opaque bands in each. Paired counts of opaque bands agreed in all cases. Therefore, the left sagittal otolith was used for age estimation unless missing, broken, or illegible, in which case the right sagitta, if available, was substituted for age analysis. Whole left sagittae were weighed on a microbalance to the nearest milligram to evaluate otolith weight as a predictor of age. Sex-specific linear regressions were fitted to otolith weight and age data and were compared by using analysis of covariance (Snedecor and Cochran, 1967); degree of significance set at $\alpha = 0.05$. Sagittae were embedded in Spurr (Secor et al., 1992) and sectioned through the core along a transverse, dorsoventral plane with a Buehler Isomet low-speed saw containing a diamond wafering blade. Two or three thin-sections (0.3 mm) were mounted on a microscope slide with CrystalBond 509 adhesive, sanded with wet 600- and 1500-grade sandpaper, polished on a felt wheel with 0.3 µm alumina micropolish, then examined under a binocular dissecting microscope at 20–40× magnification with transmitted light.

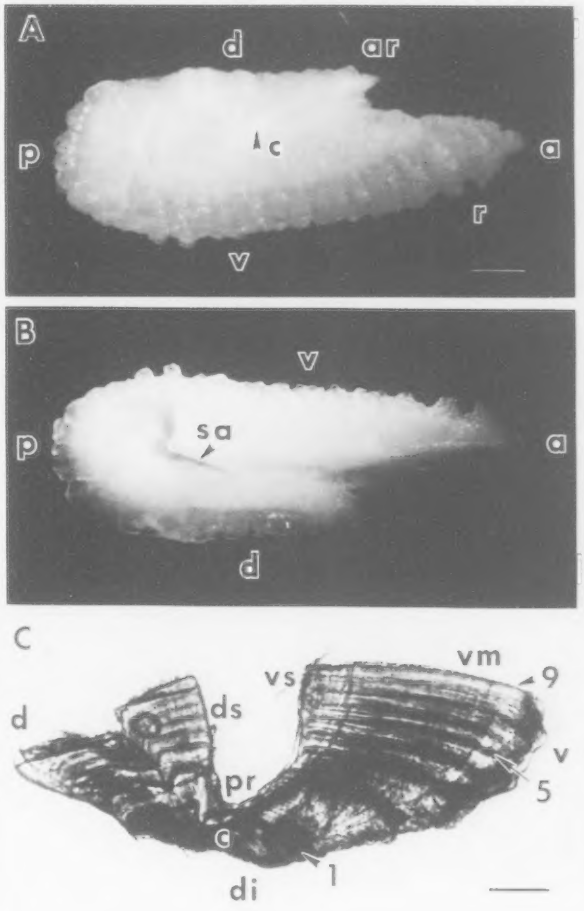


Figure 2

Whole (**A** and **B**) and sectioned (**C**) sagittal otolith from an age 9 (1621 mm FL) female cobia, *Rachycentron canadum*. The otolith's distal (A) and proximal (B) surfaces were viewed with reflected light, and C was viewed with transmitted light. Labels for A and B: a = anterior; p = posterior; d = dorsal; v = ventral; c = core; r = rostrum; ar = antirostrum; sa = sulcus. Labels for C: d = dorsal; v = ventral; di = distal; pr = proximal; c = core; ds = dorsal sulcal ridge; vs = ventral sulcal ridge; vm = ventral margin. Numbers indicate selected annuli. Scale bars = 1.00 mm for A and B; 0.50 mm for C.

Three experienced readers independently counted opaque bands from the core to the outer otolith margin. Opaque bands were most distinct and easily counted in the midportion of the ventral lobe of a section, and our analyses were made in that region (Fig. 2). Opaque bands were often obscured at the

core or confluence with the sulcus acousticus. Opaque bands were initially counted as annuli until they could be properly validated. Annuli were counted without reference to fish length or date of capture. Where counts disagreed, otolith sections were re-examined jointly, and most disagreements were resolved. Unresolved counts and illegible otoliths were excluded from the analysis. Structural aberrations in otoliths judged unsuitable for age estimation included poorly defined annuli, unusual calcification, and erosion of the ventral lobe. Terminology for otolith readings followed definitions of Wilson et al. (1987).

We determined the periodicity of annulus formation and validated our ageing technique by marginal-increment analysis. As recommended by Beamish and MacFarlane (1983), all age classes were included in the analysis. Measurements for marginal-increment analysis were made in the ventral lobe of the magnified (30×) section by using a digital imaging system. Distances were measured ventrally from the sulcus along an axis passing through the center of the lobe and extending from the otolith's core to the outer margin of the section. The distance from the proximal edge of the ultimate annulus to the otolith's margin (marginal increment) was expressed as a percentage of the distance between the proximal edge of the last two annuli formed on the otolith. This procedure was adapted for age 1 fish by expressing the marginal increment as a percentage of the distance from the edge of the first annulus to a hypothetical second annulus (Crabtree et al., 1996). Mean percent marginal increments were plotted for all age groups and collection years combined by month of capture.

The von Bertalanffy (1957) theoretical growth equation, $FL_t = L_\infty(1-\exp[-K(t-t_0)])$, was fitted to observed age-length data with the nonlinear regression procedure of Statgraphics (1994). Likelihood-ratio tests (Kimura, 1980; Cerrato, 1990) and approximate randomization tests (Helser, 1996) were used to compare growth parameter estimates for males and females. Sexed YOY were included in the growth models.

Observed ages at lengths for all years combined were used to derive an age-length key for each sex (Ricker, 1975). Aged fish (n=565) were assigned to 50-mm length intervals, and age distribution (as percent) was then calculated for each size interval. Age-length keys were used to convert length frequencies to age frequencies by assigning ages to unaged fish ≥838 mm FL from which a catch curve (Ricker, 1975) was constructed for 1987–92. We estimated instantaneous total mortality (Z) by catch curve analysis (Beverton and Holt, 1957; Everhart and Youngs, 1981) based on fully recruited fish.

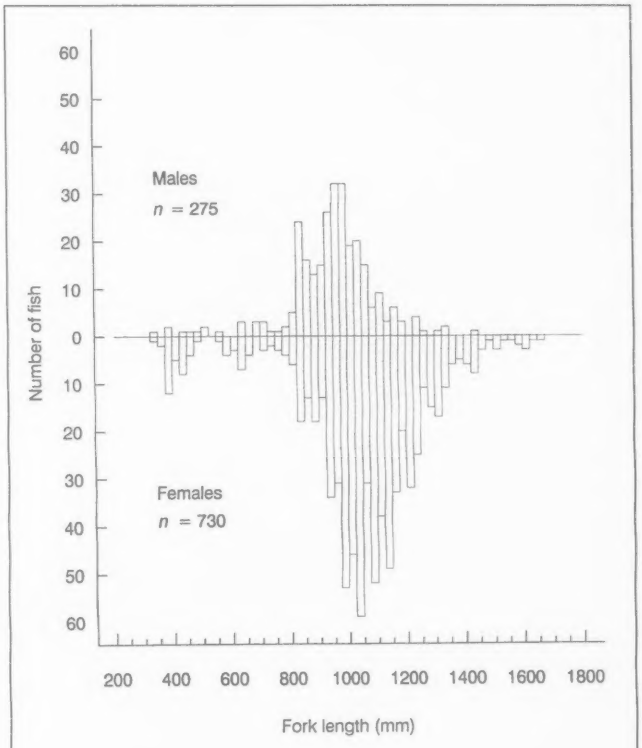


Figure 3

Length-frequency distributions (25 mm increments) for cobia, *Rachycentron canadum*, from the northeastern Gulf of Mexico collected during 1987–95.

Results

We examined 1005 cobia that ranged from 335 to 1651 mm FL, 33 of which were YOY (age 0) and ranged from 335 to 510 mm FL. External sexual dimorphism was not evident in *R. canadum*. Males (n=275) ranged from 345 to 1450 mm FL (mean=952 mm) and from 0.3–29.0 kg (mean=10.5 kg); females (n=730) ranged from 335 to 1651 mm FL (mean=1050 mm) and from 0.3 to 62.2 kg (mean=16.6 kg). The length-frequency distributions of males and females (Fig. 3) were significantly different (Kolmogorov-Smirnov two-sample test, d=0.432, P<0.05). Females

were significantly larger than males (Mann-Whitney U-test, $P<0.001$), and 85% of fish ≥1000 mm were female. The sex ratio of 1:2.7 was significantly different from 1:1 ($\chi^2=205.8$, df=1, $P<0.0001$).

Neither slopes (ANCOVA, df=914; $F=2.156$, $P=0.142$) nor elevations (ANCOVA, df=914, $F=2.334$, $P=0.127$) of the length-weight regressions by sex were found to be significantly different; therefore, data were pooled and one relationship established (Table 1; Fig. 4). Weight was approximately a cubic function of length, implying nearly isometric growth. The relationships between FL and TL are presented in Table 1.

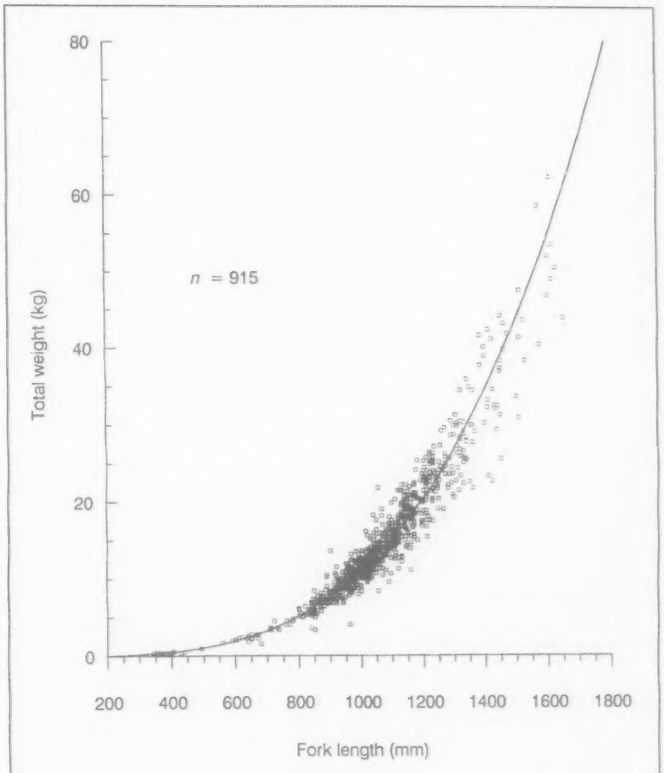


Figure 4

Length-weight relationship for cobia, *Rachycentron canadum*, from the northeastern Gulf of Mexico.

When viewed with transmitted light, thin-sectioned sagittae revealed a pattern of distinct, alternating narrow opaque and wide translucent bands (Fig 2). The distance between the first two opaque bands distally from the core typically was wider than the distance between subsequent opaque bands. Mean marginal increment analysis (Fig. 5) demonstrated that April through August was the time of annulus formation and suggested that opaque bands form once each year. All otoliths exhibited a zone of translucent material beyond the last annulus from September through February. Mean increment was minimal during June and increased to a maximum in February (no samples were collected during December). The sample size was too small to plot marginal increments for each year and age-group separately; however, a visual examination of the data indicated that marginal increments for individual years 1987–90 and age-classes 2–5 were similar, with a consistent seasonal minimum during summer. Timing of annulus formation was similar for each sex.

Of the 645 left sagittae processed for age estimates, 187 (29%) were judged illegible. Right sagittae from 168 of the latter group were available and processed, and 76% (128/168) were readable. Readers agreed on ages for 96% (565/586) of usable otoliths, 170 males (range 345–1330 mm FL) and 395 females (range 335–1651 mm FL). Only 21 (4%) of the usable otoliths were rejected because of disagreements among readings, owing primarily to disparities over the presence of an annulus adjacent to the core or at the otolith's margin. Of the sagittae found acceptable for age estimations, 33 were from YOY (335–510 mm) and 42 were from age 1 fish (493–910 mm). Ten age 1 fish were 838 mm (minimum legal size) or larger. Most (n=463, 82%) of the 565 fish that we aged were estimated to be ages 2–5 (27% age 2; 29% age 3; 17% age 4; and 9% age 5). Age 6 fish and older were conspicuously uncommon. There was a significant difference between the age-frequency distributions of males and females (Kolmogorov-Smirnov two-sample test, dn=0.308, $P<0.05$). An age 11 female (1568 mm) and age 9 males (n=2, 1240 and 1260 mm) were the oldest cobia sampled (Table 2). Twenty five females (1170–1651 mm) were age 6 or older, but only six males (1035–1330 mm) were older than age 5 (Table 2).

Growth in length for both sexes was relatively fast through age 2, after which growth slowed gradually (Fig. 6). We found a wide range of lengths within most age groups for both sexes (Tables 3 and 4). For example, age 4 males and females ranged from 850 to 1250 mm and from 900 to 1250 mm, respectively. We also found a wide range of ages within some of the length groups. For example, the 1000 mm and 1200 mm groups of males ranged from ages 2 to 7 and from

Table 1

Length-length, length-weight, and otolith weight-age regressions for cobia, *Rachycentron canadum*, from the northeastern Gulf of Mexico. FL = fork length (mm), TL = total length (mm), WT = total weight (kg), OTWT = otolith weight (g), and AGE = age in years. Sample fork length range for length-length regressions and length-weight regressions was 345–1651 mm. Age range for the otolith weight-age regression was 1–9 for males and 1–11 for females. Values in parentheses are standard errors.

			$Y = a+bX$		
Y	X	n	a	b	r^2
FL	TL	930	9.9494 (3.5691)	0.8916 (0.0032)	0.989
TL	FL	930	1.6661 (3.9964)	1.1088 (0.0040)	0.989
$\log_{10}$WT	$\log_{10}$FL	915	–9.2445 (0.6474)	3.4287 (0.0215)	0.965
OTWT (males)	AGE	126	0.0081 (0.0012)	0.0072 (0.0003)	0.775
OTWT (females)	AGE	259	0.0006 (0.0010)	0.0110 (0.0003)	0.836

Table 2

Average observed and predicted fork lengths (mm) for male and female cobia, *Rachycentron canadum*. Numbers in parentheses are standard error and sample size.

	Males		Females	
Age (yr)	Average observed	Predicted	Average observed	Predicted
0	439 (29.6;5)		409 (6.0;28)	
1	705 (26.0;14)	709	720 (21.6;28)	713
2	885 (8.5;47)	871	956 (7.9;103)	914
3	971 (9.9;47)	976	1056 (7.2;116)	1066
4	1034 (14.2;35)	1044	1140 (10.4;64)	1183
5	1070 (16.6;16)	1089	1248 (17.6;31)	1271
6	1140 (1)	1118	1346 (37.9;7)	1339
7	1198 (86.5;3)	1136	1385 (44.0;5)	1391
8		1148	1553 (27.4;8)	1430
9	1250 (10.0;2)	1156	1507 (69.9;3)	1460
10			1613 (1)	1482
11			1568 (1)	1500

Table 3

Age-length key. Fork length (mm) composition, in percent, of male cobia by age group

Length group (50 mm)	Age in years										Number of fish
	0	1	2	3	4	5	6	7	8	9	
300	100.0										1
350											
400	100.0										1
450	100.0										2
500	50.0	50.0									2
550		100.0									1
600		100.0									2
650		100.0									2
700		100.0									4
750		100.0									1
800		11.1	83.3	5.6							18
850		4.8	66.7	19.0	9.5						21
900			40.9	50.0	9.1						22
950			20.6	50.0	29.4						34
1000			9.1	27.3	22.7	36.4		4.5			22
1050				35.3	41.2	23.5					17
1100					66.7	22.2	11.1				9
1150				50.0	50.0						4
1200					20.0	40.0		20.0		20.0	5
1250										100.0	1
1300								100.0			1
Total											170

ages 4 to 9, respectively (Table 3), whereas the 1350 mm group of females ranged from ages 5 to 9 (Table 4).

The results of likelihood-ratio tests showed a significant difference in the overall von Bertalanffy growth models for males and females (χ^2=175.06, df=1, P<0.0001) (Table 5), a finding substantiated by approximate randomization testing of the growth models (P<0.0001). Likelihood-ratio tests showed that estimates of L_∞(χ^2=24.60, df=1, P<0.0001) and K (χ^2=7.02, df=1, P=0.008) were signifantly different between sexes, however, t_0 was not significantly different (χ^2=–0.11, df=1, P=0.752). Growth parameters indicated that females achieved a greater theoretical asymptotic length and grew at a faster rate than males. Predicted lengths-at-age derived by the von Bertalanffy equations agreed with observed lengths, except for age 9 males (n=2) and age 8 and 10 females (n=12) (Table 2), where observed lengths were considerably larger than those predicted. Average observed lengths-at-age for females were greater than those of males for age 1 and older (Table 2), and predicted lengths of females were greater than those of males for all ages.

Otolith weight was significantly related to age (Fig. 7), and the slopes of the otolith weight-age regressions for males and females (Table 1) were significantly different (ANCOVA , df=385, F=34.13, P<0.0001).

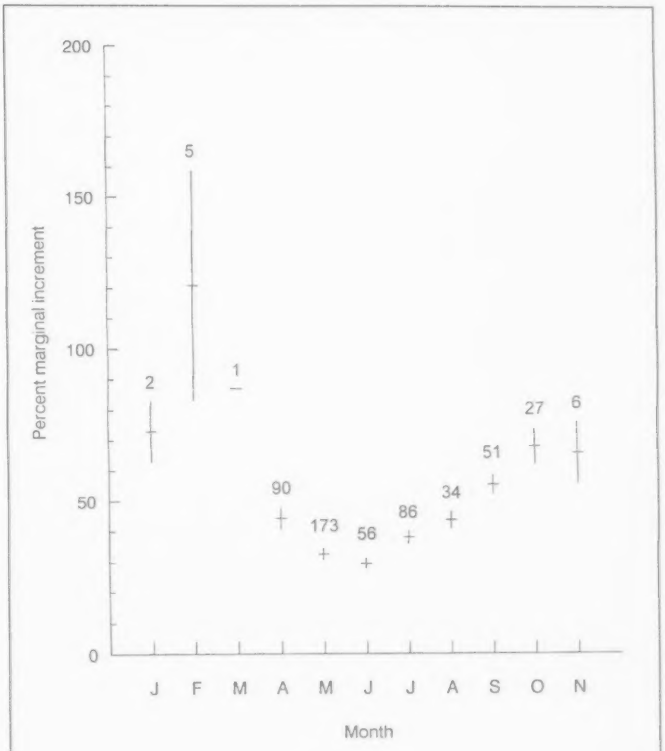


Figure 5

Monthly mean percent marginal increment for cobia, *Rachycentron canadum*. Vertical lines represent ±1 SE. Numbers above vertical lines represent sample size.

Age-length keys were constructed to estimate the age structure of legal-sized cobia (≥838 mm FL) caught from 1987 to 92 (Fig. 8) which we believe was representative of the northeastern Gulf recreational fishery. Most (84%) of those fish were age 2–4, whereas age 3 represented 37% of the catch. Age at full recruitment to the fishery was age 4 (modal age plus one). Ages 1–3 represented 66% of the fishery, age 4 represented 19%, and ages 5–11 only 15%. The instantaneous rate of total mortality (Z) estimated by our catch curve analysis for ages 4–8 was 0.75 (Fig. 9).

Discussion

Despite acquiring many of our cobia samples at fishing tournaments, we believe our overall collections reflect the recreational hook-and-line fishery for cobia in the northeastern Gulf during the late 1980s and early 1990s. Although anglers typically enter large fish in tournaments, substantial numbers of small fish were also entered during the competitions, particularly if aggregate weight awards were presented during multiday competitions. We frequently sampled anglers' entire catch which included small fish not entered in competition. Nontournament fish were also examined at docks and marinas, and these specimens ranged from less than minimum legal size to some of the largest fish that we encountered.

Although the length-weight relationships between the sexes did not differ significantly, females were typically larger than males. Thompson et al.[3] reported similar results for cobia taken off western Louisiana. In our study, females predominated (2.7:1 overall sex ratio) during all study years. Females were dominant in all age groups, and the magnitude of that dominance varied with increasing age. During a five-year study (1987–91) of cobia from western Louisiana waters (west of the Mississippi River delta), Thompson et al.[3] reported an overall sex ratio of 2.1:1 that was skewed towards males (464,

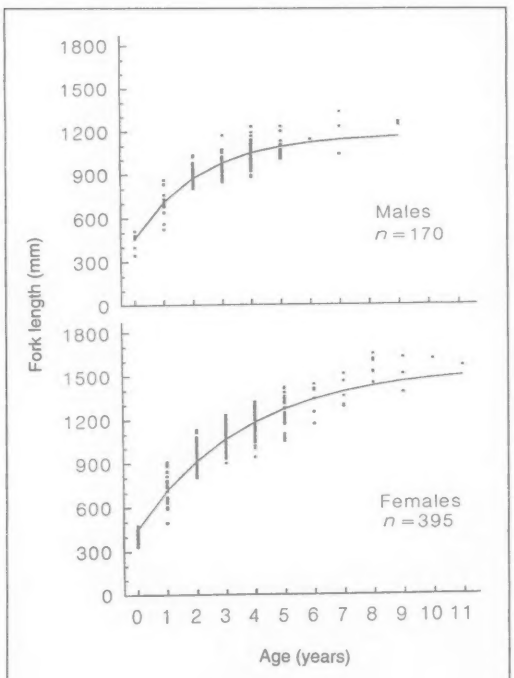


Figure 6

Observed and predicted lengths from the von Bertalanffy growth model for male and female cobia, *Rachycentron canadum*.

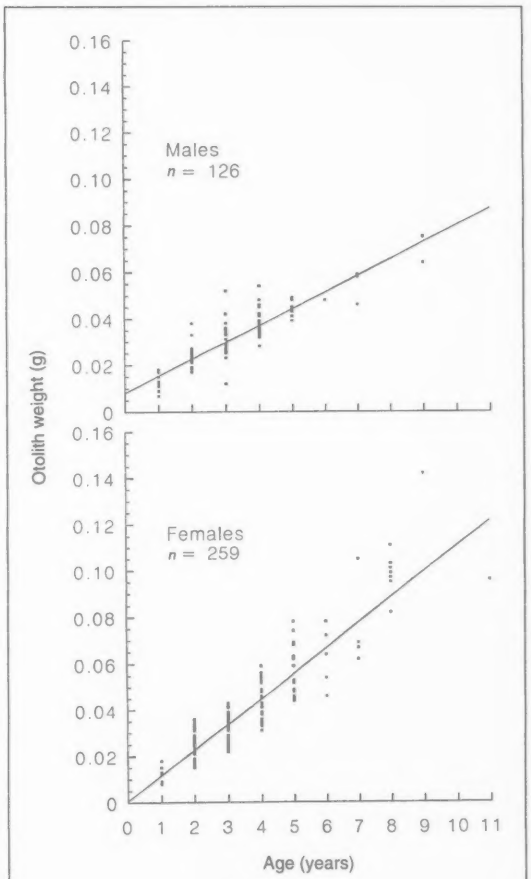


Figure 7

Sagittal weight-age relationship for male and female cobia, *Rachycentron canadum*.

males; 218 females) for each year. Because our study and that by Thompson et al.[3] were conducted concurrently, we are unable to explain this discrepancy, except to suggest differential segregation or a higher mortality for males east of the delta.

Sagittal otoliths were determined to be valid ageing structures for *R. canadum*, and alternating opaque and translucent bands were most conspicuous in the ventral lobe of otolith thin-sections. Annuli were not uniformly visible in thin-sections for some fish and were occasionally obscured along the ventral sulcal ridge, particularly for fish age 5 and older. Marginal-increment analysis indicated that annuli formed once per year during April–August. Therefore, age in years for cobia was presumed equal to the number of opaque bands observed in sectioned sagittae, findings that agree with those of Thompson et al.[3] off Louisiana and Smith (1995) off North Carolina. Because cobia are infrequently caught in northeastern Gulf waters during the winter, the scarcity of otolith samples from November through March precluded us from making an unequivocal assertion on the annual nature of opaque band formation. However, thin-sectioned sagittae from seven cobia caught in the Florida Keys during January 1991 and sampled dockside by us showed a substantial zone of translucent material extending from the distal edge of the last opaque band to the otolith margin. This finding suggests that winter annulus formation does not occur in the otoliths of cobia from south Florida waters (cobia that may migrate into northern Gulf waters in spring).

Although the timing of annulus formation coincides with the cobia's spawning season in the northern Gulf (Biesiot et al., 1994; Lotz et al., 1996), annulus deposition may be more related to cobia migration into the northern Gulf in spring. We found that sagittae of several sexually mature cobia sampled in April (early part of the spawning season) already showed opaque bands, as did sexually immature fish in spring. The relationship of annulus formation to

Table 4

Age-length key. Fork length (mm) composition, in percent, of female cobia by age group

Length group (50 mm)	Age in years												Number of fish
	0	1	2	3	4	5	6	7	8	9	10	11	
300	100.0												1
350	100.0												8
400	100.0												17
450	66.7	33.3											3
500													
550		100.0											1
600		100.0											7
650		100.0											5
700		100.0											3
750		100.0											3
800		25.0	75.0										12
850		19.0	81.0										21
900		3.3	66.7	26.7	3.3								30
950			52.2	47.8									46
1000			40.0	47.3	12.7								55
1050			12.2	53.1	28.6	6.1							49
1100			13.2	39.5	44.7	2.6							38
1150				46.4	28.6	21.4	3.6						28
1200				28.6	42.8	28.6							21
1250					40.0	40.0	10.0	10.0					10
1300					33.4	50.0	8.3	8.3					12
1350						60.0		20.0		20.0			5
1400						28.6	57.1		14.3				7
1450								50.0	50.0				2
1500								25.0	50.0	25.0			4
1550												100.0	1
1600									60.0	20.0	20.0		5
1650									100.0				1
Total													395

Table 5

Parameter estimates for the von Bertalanffy growth model for cobia, *Rachycentron canadum*, from U.S. waters. Values shown in parentheses are standard errors. — = not reported by author(s).

Area	Sex	n	L_∞	K	t_0	r^2	Structure	Authors
Virginia[1]	M	—	121	0.28	−0.06	—	scales	Richards, 1967
	F	—	164	0.23	−0.08			
North Carolina[1]	M	116	105	0.37	−1.08	—	otoliths	Smith, 1995
			(1.85)	(0.04)	(0.29)			
	F	92	135	0.24	−1.53			
			(3.82)	(0.03)	(0.39)			
Western Louisiana[2]	M	—	1,132	0.49	−0.49	—	otoliths	Thompson et al.[3]
	F	—	1,294	0.56	0.11			
Northeastern Gulf of Mexico[2]	M	170	1,170.7	0.432	−1.150	0.78	otoliths	This study
			(28.08)	(0.046)	(0.173)			
	F	395	1,555.0	0.272	−1.254	0.87		
			(35.14)	(0.017)	(0.092)			

[1] L_∞ estimates reported in centimeters.
[2] L_∞ estimates reported in millimeters.
[3] See Footnote 3 in text for this source.

migration has been suggested for swordfish (Berkeley and Houde, 1983; Tserpes and Tsimenides, 1995) and Atlantic bluefin tuna (Compean-Jimenez and Bard, 1983). Other authors (Nelson and Manooch, 1982; Sturm et al., 1989; Beckman et al., 1990; Ferreira and Russ, 1994) also suggested that reproduction may not be the sole determining factor and commented on the physiological nature of annulus formation and the importance of environmental factors.

Longevity of male and female cobia differed considerably. Males older than age 7 were rare, and maximum age was 9. Females older than age 8 were rare, and maximum age was 11. Maximum ages of cobia from Louisiana (age 10, Thompson et al.[3]) and Virginia (age 10, Richards, 1967) were similar to our observations. However, Smith (1995) reported a maximum age of 14 for males and age 13 for females for cobia from North Carolina. We also found, as did Richards (1967) and Smith (1995), that mean observed lengths at age for females were larger than those for males for all age classes, except age 0 fish.

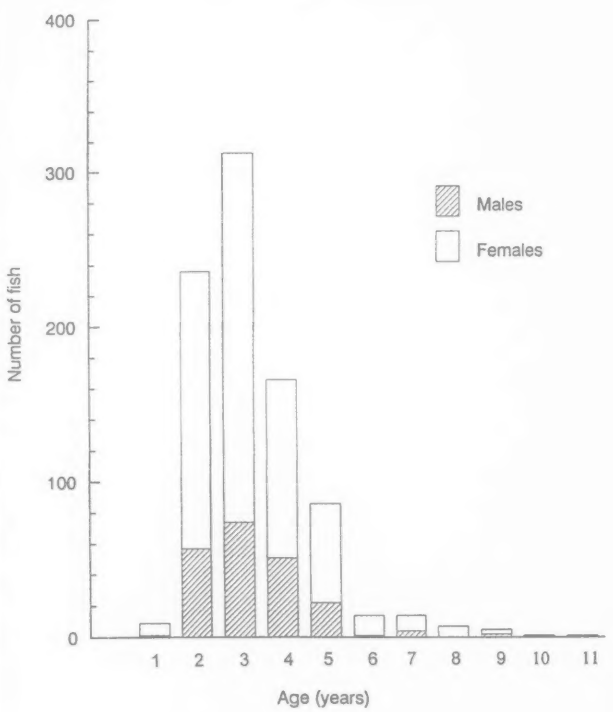


Figure 8

Age structure of cobia, *Rachycentron canadum*, ≥838 mm FL (regulation minimum size) in the northeastern Gulf of Mexico recreational hook-and-line fishery, 1987–92. n=992

Considerable variation in size was observed within most age groups, including YOY, for both males and females, which, according to Goodwin and Johnson (1986), is not unusual for warm-water fishes. The variation in size makes it difficult to estimate precisely the age of cobia from length alone. For example, our largest cobia weighed 62.2 kg, which was slightly greater than the all-tackle world record weight for cobia (61.5 kg) reported by the International Game Fish Association (1997). At a fork length of 1610 mm and at age 8, this specimen was neither the longest fish in our sample nor the oldest. A prolonged spawning season and multiple spawnings characteristic of cobia (Lotz et al., 1996) probably account for the wide variation in size of YOY cobia and other age groups as well. Annual growth was most rapid through age 2 for both sexes, then gradually decreased thereafter, particularly for females.

Otolith weight was a good predictor of age, accounted for 78% and 84% of the variability in age of male and female cobia, respectively, and explained as much variation in age as fork length in the von Bertalanffy model for each sex.

Our estimates of growth parameters are the only estimates available for *R. canadum* in the northeastern Gulf. We found that the von Bertalanffy theoretical growth models for males and females were significantly different, as did Thompson et al.[3] Lengths predicted from the theoretical growth curves agreed with the average observed lengths. Theoretical asymptotic lengths seemed realistic, even though few fish >1200 mm were sampled. Theoretical growth coefficients (L_∞ and t_0) reported by Thompson et al.[3] for cobia from Louisiana were smaller than our estimates (Table 5), although their estimates of K were larger, particularly for females. Asymptotic lengths for males and females taken off Virginia (Richards, 1977) were considerably larger than L_∞ values reported by Smith (1995) for cobia from North Carolina, values reported by Thompson et al.[3] for cobia from Louisiana and our study (Table 5), although our asymptotic length for males was similar to that in Richards' (1967) study. The differences in estimates of growth coefficients for cobia throughout their range in U.S. waters may be due to methodological differences, e.g. sectioned otoliths (this study) versus scales (Richards, 1967), or differences in geographical coverage. Nevertheless, we believe our growth parameter estimates are appropriate for

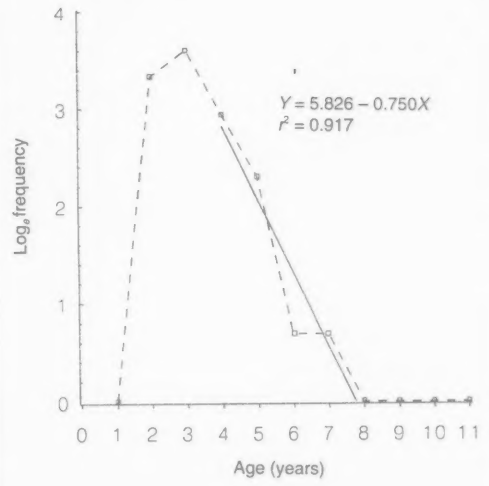


Figure 9

Length-converted catch curve for cobia taken in the northeastern Gulf of Mexico recreational fishery. The solid line described by the equation ($Y=a+bX$) indicates the age range used in regression estimates of instantaneous total mortality (Z). Z is equal to the absolute value of the slope (b) of the regression line.

use in assessment studies of cobia from the northeastern Gulf.

Cobia were fully recruited to the recreational fishery in the northeastern Gulf at age 4. Catch curve analysis predicted a Z of 0.75. A fairly broad age structure and a low value for Z suggest that the northeastern Gulf population of cobia is reasonably healthy. We believe our estimate of Z is reliable, although several authors (Rounsefell and Everhart, 1953; Johnson, et al., 1983; and Manooch et al., 1987) caution against using catch curves to predict mortality for migratory pelagic species because, in part, such predictions are subject to a variety of assumptions, including a constant recruitment and mortality for each year and year class comprising a pooled data set. The popularity of cobia warrants continued monitoring of population age structure and growth parameters of this valuable gamefish in the northern Gulf.

Acknowledgments

We are indebted to the anglers who allowed us to sample their catch of cobia. We thank Barbara Palko, formerly of the National Marine Fisheries Service (NMFS), Panama City (Florida) Laboratory, for making numerous specimens available to us. We express our appreciation to Thomas McIlwain of the NMFS and Richard Leard of the Gulf of Mexico Fishery Management Council for their encouragement and advocacy of our work, particularly in the initial stages of the study. Many thanks to our colleagues in the Marine Fisheries Division of the Mississippi Department of Marine Resources. Chuck Wilson, Bruce Thompson, and Louise Stanley of Louisiana State University, Coastal Fisheries Institute, provided valuable advice and great inspiration. We express our sincere gratitude to Mike Allen and Dyan Wilson for their diligence at the otolith saw and their assistance in reading otoliths. We acknowledge the many contributions of T. J. Becker, the archetypal tournament sampler. We thank Robin Overstreet for photographing the otoliths shown in this manuscript and for sharing with us his interest in the biology of cobia over many years. Many other individuals participated in portions of this study including the following Gulf Coast Research Laboratory personnel: Don Barnes, Lisa Engel, Dale Fremin, Nikola Garber, Nate Jordan, David Lee, Jeffery Lotz, Terry McBee, Casey Nicholson, Steve Vanderkooy, and Mike Zuber. We also offer thanks to Michael Murphy and Roy Crabtree of the Florida Marine Research Institute and to James Duffey of the Alabama Department of Conservation and Natural Resources for their valued advice and assistance on statistical treatment of the data. We recognize colleagues Patricia Biesiot of the University of Southern Mississippi, and Joe Smith and John Merriner of the NMFS Beaufort (North Carolina) Laboratory who share with us a deep appreciation for this great fish. We thank three anonymous reviewers and the scientific editor for their extremely helpful comments and suggestions. This work was supported in part by funding from Federal Aid in Sport Fish Restoration, Department of the Interior, U. S. Fish and Wildlife Service, Atlanta, GA, Project No. F-91, and the Mississippi Department of Marine Resources, Biloxi, Mississippi.

Literature cited

Beamish, R. J., and G. A. MacFarlane
1983. The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112:735–743.

Beckman, D. W., A. L. Stanley, J. H. Render, and C. A. Wilson.
1990. Age and growth of black drum in Louisiana waters of the Gulf of Mexico. Trans. Am. Fish. Soc. 119:537–544.

Berkeley, S. A., and E. D. Houde.
1983. Age determination of the broadbill swordfish, *Xiphias gladius*, from the Straits of Florida, using anal fin spine sections. U. S. Dep. Commer., NOAA Tech. Rep. NMFS 8:137–143.

Beverton, F. J. H., and S. J. Holt.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric., Fish. Food (G. B.), Ser. II, 19, 533 p.

Biesiot, P. M., R. M. Caylor, and J. S. Franks.
1994. Biochemical and histological changes during ovarian development of cobia, *Rachycentron canadum*, from the northern Gulf of Mexico. Fish. Bull. 92:686–696.

Briggs, J. C.
1958. A list of Florida fishes and their distribution. Bull. Fla. State Mus., Biol. Sci. 2:221– 318.
1960. Fishes of worldwide (circumtropical) distribution. Copeia 1960(3):171–180.

Cerrato, R. M.
1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. Can. J. Fish. Aquat. Sci. 47:1,416–1,426.

Compean-Jimenez, G., and F. X. Bard.
1983. Growth increments on dorsal spines of eastern Atlantic bluefin tuna, *Thunnus thynnus*, and their possible relation to migration patterns. *In* E. D. Prince and L. M. Pulos (eds.), Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes and sharks, p.111–115. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8.

Crabtree, R. E., C. W. Harnden, D. Snodgrass, and C. Stevens.
1996. Age, growth and mortality of bonefish, *Albula vulpes*, from the waters of the Florida Keys. Fish. Bull. 94:442–451.

Dawson, C. E.
1971. Occurrence and description of prejuvenile and early juvenile Gulf of Mexico cobia, *Rachycentron canadum*. Copeia 1960(3):171–180.

Ditty, J. G., and R. F. Shaw.
1992. Larval development, distribution, and ecology of cobia, *Rachycentron canadum* (Family:Rachycentridae), in the northern Gulf of Mexico. Fish. Bull. 90:668–677.

Everhart, H. W., and W. D. Youngs.
1981. Principles of fishery science. Cornell Univ. Press, Ithaca, New York, NY, 349 p.

Ferreira, B. P., and G. R. Russ.
1994. Age validation and estimation of growth rate of the coral trout, *Plectropomus leopardus* (Lacepede 1802), from Lizard Island, Northern Great Barrier Reef. Fish. Bull. 92:46–57.

Franks, J. S.
1995. A pugheaded cobia (*Rachycentron canadum*) from the northcentral Gulf of Mexico. Gulf Res. Rep. 9(2):143–145.

Franks, J. S., N. M. Garber, and J. R. Warren
1996. Stomach contents of juvenile cobia, *Rachycentron canadum*, from the northern Gulf of Mexico. Fish. Bull. 94:374–380.

Franks, J. S., M. H. Zuber, and T. D. McIlwain.
1991. Trends in seasonal movements of cobia, *Rachycentron canadum*, tagged and released in the northern Gulf of Mexico. J. Miss. Acad. Sci. 36(1):55.

Goodwin, J. M., and Johnson A. G.
1986. Age, growth, and mortality of blue runner, *Caranx crysos*, from the northern Gulf of Mexico. Northeast Gulf Sci. 8(2):107–114.

Hassler, W. W., and R. P. Rainville.
1975. Techniques for hatching and rearing cobia, *Rachycentron canadum*, through larval and juvenile stages. Univ. N.C. Sea Grant Coll. Prog., UNC-SG-75-30, Raleigh, NC, 26 p.

Helser, T. E.
1996. Growth of silver hake within the U.S. continental shelf ecosystem of the northwest Atlantic Ocean. J. Fish. Biol. 48:1,059–1,073.

Howse, H. D., J. S. Franks, and R. F. Welford.
1975. Pericardial adhesions in the cobia (*Rachycentron canadum*) (Linnaeus). Gulf Res. Rep. 5(1):61–62.

Howse, H. D., R. M. Overstreet, W. E. Hawkins, and J. S. Franks.
1992. Ubiquitous perivenous smooth muscle cords in viscera of the teleost *Rachycentron canadum*, with special emphasis on liver. J. Morphol. 212:175–189.

Hrincevich, A. W.
1993. Analysis of cobia *Rachycentron canadum* population structure in the northern Gulf of Mexico using mitochondrial DNA. M.S. thesis, Univ. Southern Miss., Hattiesburg, MS, 91 p.

International Game Fish Association.
1997. World record game fishes. International Game Fish Association, Pompano Beach, Florida, 352 p.

Johnson, A. G., W. A. Fable, M. L. Williams, and L. E. Barger.
1983. Age, growth, and mortality of king mackerel, *Scomberomorus cavalla*, from the southeastern United States. Fish. Bull. 81(1):97–106.

Joseph, E. B., J. J. Norcross, and W. H. Massmann.
1964. Spawning of the cobia, *Rachycentron canadum*, in the Chesapeake Bay area, with observations of juvenile specimens. Chesapeake Sci. 5:67–71.

Kimura, D. K.
1980. Likelihood methods for the von Bertalanffy growth curve. Fish. Bull. 77(4):765–776.

Knapp, F. T.
1949. Menhaden utilization in relation to the conservation of food and game fishes of the Texas Gulf Coast. Trans. Am. Fish. Soc.79:137–144.

Knapp, F. T.
1951. Food habits of the sergeantfish, *Rachycentron canadus*. Copeia 1951:101–102.

Lotz, J. M., R. M. Overstreet, and J. S. Franks.
1996. Gonadal maturation in the cobia, *Rachycentron canadum*, from the northcentral Gulf of Mexico. Gulf Res. Rep. 9(3):147–159.

Manooch, C. S., S. P. Naughton, C. B. Grimes, and L. Trent.
1987. Age and growth of king mackerel, *Scomberomorus cavalla*, from the U. S. Gulf of Mexico. Mar. Fish. Rev. 49(2):102–108.

Meyer, G. H., and J. S. Franks.
1996. Food of cobia, *Rachycentron canadum*, from the northcentral Gulf of Mexico. Gulf Res. Rep. 9(3):161–167.

Miles, D. W.
1949. A study of the food habits of the fishes of the Aransas Bay area. M.S. thesis, Univ. Houston, TX, 70 p.

Nelson, R. S., and C. S. Manooch.
1982. Growth and mortality of red snappers in the west-central Atlantic Ocean and northern Gulf of Mexico. Trans. Am. Fish. Soc. 111:465–475.

Richards, C. E.
1967. Age, growth and fecundity of the cobia, *Rachycentron canadum*, from the Chesapeake Bay and adjacent Mid-Atlantic waters. Trans. Am. Fish. Soc. 96:343–350.
1977. Cobia (*Rachycentron canadum*) tagging within Chesapeake Bay and updating of growth equations. Chesapeake Sci. 18:310–311.

Ricker, W. E.
1975. Computations and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.

Rounsefell, G. A., and W. H. Everhart.
1953. Fishery science: its methods and applications. John Wiley and Sons, Inc., New York, NY, 444 p.

Secor, D. H., J. M. Dean, and E. H. Laban.
1992. Otolith removal and preparation for microstructural examination. *In* D. K. Stevenson and S. E. Campana (eds.), Otolith microstructure examination and analysis, p. 19–57. Can. Spec. Publ. Fish. Aquat. Sci. 117.

Shaffer, R. V., and E. L. Nakamura.
1989. Synopsis of biological data on the cobia *Rachycentron canadum* (Pisces: Rachycentridae). FAO Fisheries Synop. 153 (NMFS/S 153). U.S. Dep. Commer., NOAA Tech. Rep. NMFS 82, 21 p.

Smith, J. W.
1995. Life history of cobia, *Rachycentron canadum* (Osteichthyes:Rachycentridae), in North Carolina waters. Brimleyana 23:1–23.

Snedecor, G. W. and W. C. Cochran.
1967. Statistical methods, 6th ed. Iowa State Univ. Press, Ames, IA, 593 p.

Statgraphics
1994. Statistical graphics software, ver. 7.1. Manugistics, Inc., Rockville, MD.

Sturm, M. G. de L., and P. Salter.
1989. Age, growth and reproduction of the king mackerel *Scomberomorus cavalla* (Cuvier) in Trinidad waters. Fish. Bull. 88:361–370.

Tserpes, G., and N. Tsimenides
1995. Determination of age and growth of swordfish, *Xiphias gladius* L., 1758, in the eastern Mediterranean using anal-fin spines. Fish. Bull. 93:594–602.

von Bertalanffy, L.
1957. Quantitative laws in metabolism and growth. Quart. Rev. Biol. 32:217–231.

Wilson, C. A., R. J. Beamish, E. B. Brothers, K. D. Carlander, J. M. Casselman, J. M. Dean, A. Jerald, E. D. Prince, and A. Wild.
1987. Glossary. *In* R. C. Summerfelt and G. E. Hall (eds.), Age and growth of fish, p. 527–530. Iowa State Univ. Press, Ames, Iowa.

Growth patterns in postsmolts and the nature of the marine juvenile nursery for Atlantic salmon, *Salmo salar*

Kevin D. Friedland
UMass/NOAA CMER Program
Blaisdell House, University of Massachusetts
Amherst, Massachusetts 01003
E-mail address: friedlandk@forwild.umass.edu

Jean-Denis Dutil
Ministère des Pêches et des Océans
Institut Maurice-Lamontagne
850 route de la Mer, Mont-Joli, Québec, Canada G5H 3Z4

Teresa Sadusky
National Marine Fisheries Service, NOAA
166 Water Street
Woods Hole, Massachusetts, 02543

Abstract.—We examined scale samples from historical collections of postsmolts from the Gulf of St. Lawrence, Canada, with the aim of understanding the role of estuarine and coastal habitats as a juvenile nursery for Atlantic salmon. Circuli spacing patterns were extracted from the scales of 580 postsmolts collected in the Gulf during three seasons, 1982–84. Poststratification of the samples by collection date within year suggests that in some years postsmolts remain in the Gulf throughout the entire summer growth season, whereas in other years only slower growing fish remain in these areas. Growth patterns for Gulf of St. Lawrence postsmolts were compared with patterns for returns from three salmon stocks from the southern end of the range in North America. These data suggest that in some years postsmolt growth in the Gulf is as robust as that observed for both the one seawinter (1SW) and two seawinter (2SW) returns to southern rivers. Postsmolts are believed to use oceanic nursery areas generally; thus, comparable growth between the two stock groups suggests that the Gulf may serve as an important part of the postsmolt nursery range in some years. The concept of the postsmolt nursery as a continuum between neritic and oceanic areas is essential to evaluating ocean climate and productivity effects on salmonid recruitment.

Manuscript accepted 11 August 1998.
Fish. Bull. 97:472–481 (1999).

Anadromous salmonids, such as Atlantic salmon, *Salmo salar*, use freshwater stream habitats as nursery areas for their early life history stages (Thorpe, 1994). Freshwater residency provides refuge from potential predators and relatively stable survival conditions for eggs and juveniles (Chaput et al., 1998). Thus, the recruitment of smolts during the freshwater phase is characterized by relatively low annual variability, most of which is attributed to the size of spawning escapements (Chadwick, 1987). As a consequence, the relationships between spawning stock abundance and recruits migrating from freshwater take on predictable forms (Chadwick, 1985; Elliott, 1993). The relationships between generations of spawners, however, are not as clear owing to highly variable rates of marine survival.

The first year at sea, or the postsmolt year, for Atlantic salmon is poorly understood. The transition to the marine environment is in itself a survival challenge associated with specific estuarine habitats (Levings, 1994). After postsmolts make the transition, they are believed to disperse widely in ocean surface waters. This belief stems from the facts that they are rarely caught in nearshore fishing gears and have proven difficult to capture in directed surveys. The exception has been in the Baltic area, where the spatial confines of the Baltic Sea and postsmolt recoveries in commercial fisheries have combined to produce a relative wealth of information on the distribution and survival of postsmolts in that region (Larsson, 1985; Eriksson 1994; Kuikka and Salminen 1994). The equivalent information does not exist for North Atlantic postsmolts; thus, it is critical to learn more about the basic biology of postsmolts so that informed interpretations of the patterns in salmonid population dynamics can be made.

Recoveries of North American versus European postsmolts suggest that habitat use and ecological roles may differ for the early marine stages of the two stock complexes. Recent captures of postsmolts in the Northeast Atlantic show that they are distributed over

a large oceanic region by their first summer at sea (Holm et al., 1996; Shelton et al., 1997). These distribution patterns suggest that postsmolts migrate to the northwest and may be less likely to use inshore neritic habitats. However, in the Northwest Atlantic, the few recovery data available for postsmolts suggest differing views of which habitats represent the nursery area for postsmolts. Salmon postsmolts have been reported to use estuarine waters; therefore it is possible that they possess specific behaviors to orient themselves to inshore areas during their first year at sea (Robitaille et al., 1986; Dutil and Coutu, 1988; Cunjak et al., 1989). In contrast, postsmolts have also been collected from research surveys in the Labrador Sea and indirectly from bird colonies, providing evidence that the extent of the postsmolt migration includes waters north of Newfoundland (Montevecchi et al., 1988; Reddin and Short, 1991). Recoveries of postsmolts in estuarine areas support the hypothesis that specific habitats serve as nursery areas for postsmolts, whereas recoveries in the pelagic zone support the alternative, that juveniles have thermal preferences similar to adults and do not use specific postsmolt nursery areas.

In this paper we re-examined material collected by Dutil and Coutu (1988) with the aim of understanding the use of the Gulf of St. Lawrence by salmon postsmolts. Specifically, we collected circuli spacing data from salmon scales to address the following questions: 1) Are postsmolts retained in the Gulf of St. Lawrence during the postsmolt growth season or are they transient in the area?; and 2) Do postsmolts recovered in the Gulf exhibit growth patterns similar to postsmolts from other stocks? The answers to these questions will hopefully allow us to make some inference about the nature of the nursery for Atlantic salmon and salmonids in general.

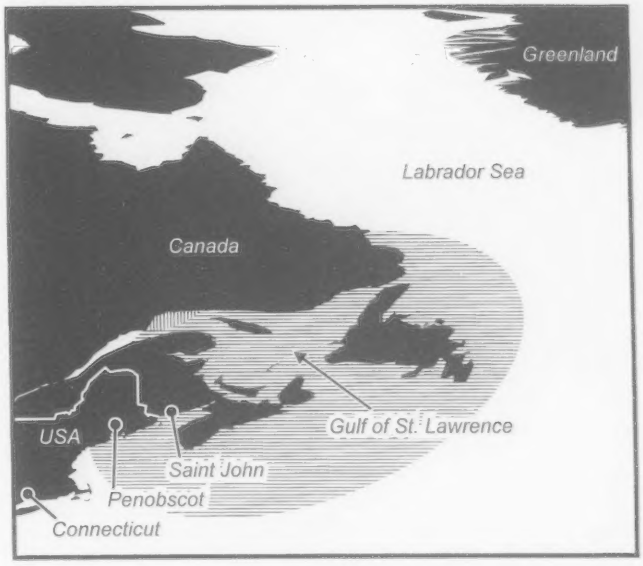


Figure 1

Map of Northwest Atlantic area showing postsmolt habitat for stocks in the Gulf of St. Lawrence and south (horizontal hatching) and sampling area for Gulf of St. Lawrence postsmolts (vertical hatching).

Table 1

Sample sizes for circuli analysis by stock group and age of capture.

		Smolt year		
Stock	Age	1982	1983	1984
Connecticut	2SW	52	81	110
Penobscot	1SW	65	63	57
	2SW	75	75	40
St. John	1SW	84	65	51
	2SW	81	67	54
Gulf of St. Lawrence	Post smolt	372	154	54

Material and methods

We collected scale circuli spacing data representative of postsmolt growth for juvenile salmon captured in the Gulf of St. Lawrence and for three index stocks from the southern portion of the range of salmon in North America. Gulf of St. Lawrence postsmolt salmon were collected in 1982–84 and were originally reported in Dutil and Coutu (1988). These postsmolts were captured in experimental gill nets along the northwest shore of the Gulf during the months from August to October (Fig. 1). Data for comparative purposes come from the returning adults of hatchery origin fish from the Connecticut, Penobscot, and Saint John rivers, all located south of the Gulf of St. Lawrence (Fig. 1). Data for the Connecticut and Penobscot rivers have been presented earlier (Friedland et al., 1996b); whereas, the Saint John data are newly reported here. Sample sizes sorted by smolt year of migration to sea and age of maturity are reported in Table 1. The low number of 1SW returns to the Connecticut River did not provide sufficient samples for inclusion in our study.

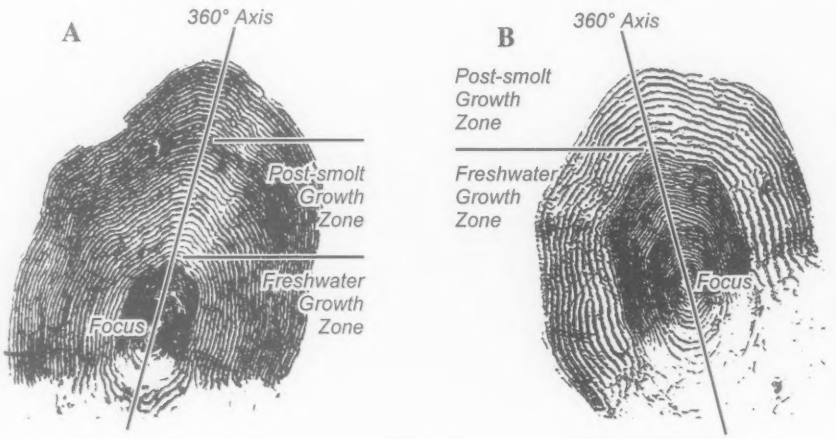


Figure 2

Illustrations of Atlantic salmon scales from a 1SW salmon (**A**) and a postsmolt salmon (**B**). Focus of each scale is marked; freshwater growth zone extends from focus to start of marine growth; and postsmolt growth zone extends to first winter annuli. The figures are not in scale.

Postsmolt growth was interpreted from circuli spacing patterns deposited during the postsmolt year. Scales were cleaned and mounted between glass slides and the spacings of scale circuli were measured with a Bioscan Optimas image processing system. The first spacing was measured between the first circulus of the postsmolt growth zone and the next circulus and continued with successive circuli pairs. For maturing fish returning to their natal river after at least one winter at sea, the measurements were made through the first seawinter annulus of the scale and thus captured the entire postsmolt growth zone (Fig. 2A). For fish captured as postsmolts, measurements were taken to the edge of the scale (Fig. 2B). Thus, only part of the data collected from maturing fish was needed for comparison with the postsmolts. Measurements were made on a single scale from each specimen at a pixel resolution of 0.004 mm along the 360° axis of the scale.

Return rates by sea-age and fraction of the smolt cohort maturing after one seawinter (1SW) were computed for the three stocks used for comparison. Return rates are simple percentages of the number of returns-at-age to the number of smolts released. Return rates for the Connecticut and Penobscot stocks originally reported in Friedland et al. (1996b) are updated here. Return rates for the Saint John stock were computed similarly and are based on smolt releases of 172, 145, and 206 thousand smolts for the years 1982–84, respectively. Releases over the period 1974–92 averaged approximately 200 thousand smolts annually in the Saint John system. The fraction of the smolt cohort maturing after one seawinter, the 1SW fraction, was computed with the formulae of Friedland et al. (1996b). Likewise, these data are updated for the Connecticut and Penobscot stocks and are newly reported for the Saint John stock.

Circuli spacing data for Gulf of St. Lawrence postsmolts were compared in three ways. In the first comparison, data for the postsmolt scales were compared for the period 1982–84. The spacings of the first ten circuli pairs were compared with ANOVA. This and subsequent statistical analyses were restricted to the first ten circuli pairs because most postsmolt scales did not have circuli beyond the tenth pair. As a consequence, spacing patterns for circuli pairs beyond pair number 10 were not well estimated. In the second comparison, for two of the seasons, 1982 and 1983, where sufficient samples of postsmolts were available, samples were poststratified by collection date. The poststratification was done to achieve nearly equal numbers of samples in each stratum. In 1982, three within-year strata were created: 8 to 17 August composed of 126 samples, 18 August to 5 September composed of 121 samples, and 7 September to 18 October composed of 125 samples. In 1983, two strata were created: 24 to 30 September composed of 73 samples and 1 to 11 October composed of 81 samples. Circuli spacing of the first ten circuli pairs for the poststratified groups were compared with ANOVA. For the third comparison, circuli spacing data from Gulf postsmolt scales were compared with the circuli spacing data for the three

Table 2

Results of ANOVAs testing year effect in scale circuli spacing from collections of postsmolt salmon from the Gulf of St. Lawrence from 1982 to 1984.

Spacing pair	df effect	MS effect	df error	MS error	*F*	*P*-level	
1	2	0.00291	577	0.00015	19.312	0.00	*
2	2	0.00023	577	0.00020	1.170	0.31	
3	2	0.00112	577	0.00024	4.605	0.01	*
4	2	0.00290	577	0.00021	13.491	0.00	*
5	2	0.00591	576	0.00020	28.895	0.00	*
6	2	0.00700	575	0.00017	40.579	0.00	*
7	2	0.00620	574	0.00019	33.492	0.00	*
8	2	0.00482	573	0.00015	31.914	0.00	*
9	2	0.00398	559	0.00016	24.686	0.00	*
10	2	0.00217	526	0.00016	13.521	0.00	*

comparison stocks. The data for the comparison stocks were grouped by sea-age; thus, the postsmolt scale data were compared with a total of five scale growth signals. The statistical comparison was simplified to a two-group ANOVA, namely to comparing circuli spacing of the first ten circuli pairs of the postsmolts with a combined sample of all the comparison stocks.

Results

Circuli spacing patterns for the postsmolt growth zones of Gulf of St. Lawrence postsmolts were significantly different for the three year classes we examined. Circuli spacing for the first few pairs, associated with the first few weeks in the marine environment, were similar in all three years, measuring approximately 0.050 to 0.055 mm (Fig. 3). However, beyond these initial pairs the spacings diverged into three distinct patterns. Spacings for fish captured in 1982, based on the mean spacings for pairs 4–8, were the widest, generally larger than 0.065 mm. Circuli spacings in the same region of the scale were progressively smaller for samples collected in 1983 and 1984. In 1983, most of the mean spacings did not exceed 0.060 mm and for 1984 they did not exceed 0.055 mm. ANOVA results show that the yearly spacings means were significantly different for all but one of the first ten spacing pairs (Table 2). The means for spacing pair number 2 is not significantly different because the rank order of the means changes between spacing pairs 1 and 3.

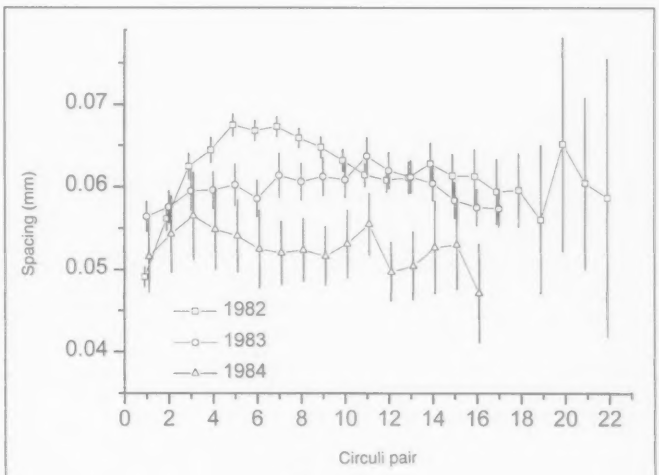


Figure 3

Circuli spacing versus circuli pair for Gulf of St. Lawrence postsmolts for three smolt year classes, 1982–84. Error bars mark 95% confidence intervals.

Within-year comparisons of Gulf of St. Lawrence samples poststratified by collection date suggest that in one year the same group or population of fish were sampled during the entire growth season; whereas, in another year, the postsmolt assemblage appeared to change during the sampling period. All three poststratified groups formed from the 1982 data showed a similar pattern of circuli spacing versus circuli pair through pair number 12 (Fig. 4A). After circuli pair 12, the mean spacing for the three poststratified groups began to diverge; however, the mean spacing for these circuli pairs was estimated

with low precision owing to the small sample sizes available. No significant differences existed between the spacing means for circuli pairs 1–10 (Table 3). In contrast, the data for 1983 showed that spacing patterns and growth were different for early versus late season collections. Fish collected in September had wider circuli spacings for circuli pairs 4–10 than fish collected in October (Fig. 4B). The September samples had mean spacings generally above 0.0625 mm; whereas, the October samples had mean spacings generally below 0.06 mm. Most of the statistical comparisons between the poststratified groups were significant at either P=0.05 or P=0.1 (Table 3).

The seasonal pattern in circuli spacing for Gulf of St. Lawrence postsmolts was similar to the patterns observed for the some of the comparison stocks by year, and dissimilar in other cases. For smolt year 1982, Gulf of St. Lawrence postsmolts and Penobscot and Saint John returns showed similar seasonal patterns of circuli spacing versus circuli pair (Fig. 5A). This comparison included both the 1SW and 2SW maturity groups within a stock. The pattern of mean circuli spacing for Connecticut River 2SW returns was different from that for the other stocks and showed an ontogenetic trajectory of narrower spacings with age. When compared statistically, mean spacings for Gulf postsmolts were significantly higher and lower than the mean for the three comparison stocks (Table 4). The mean spacing for circuli pair 1 was significantly lower for Gulf postsmolts compared with the other stocks, but the relationship between stock circuli spacing changed for pairs 4–8 as the rank order changed. The rank order changed again by circuli pair 10. In 1983, the spacing pattern for the postsmolts could not be distinguished graphically from the combined signals for the other stocks (Fig. 5B), which is supported by statistical comparison as well (Table 4). Again, the Connecticut River stock had the narrowest spacings, whereas the widest spacings were observed in Penobscot and Saint John fish.

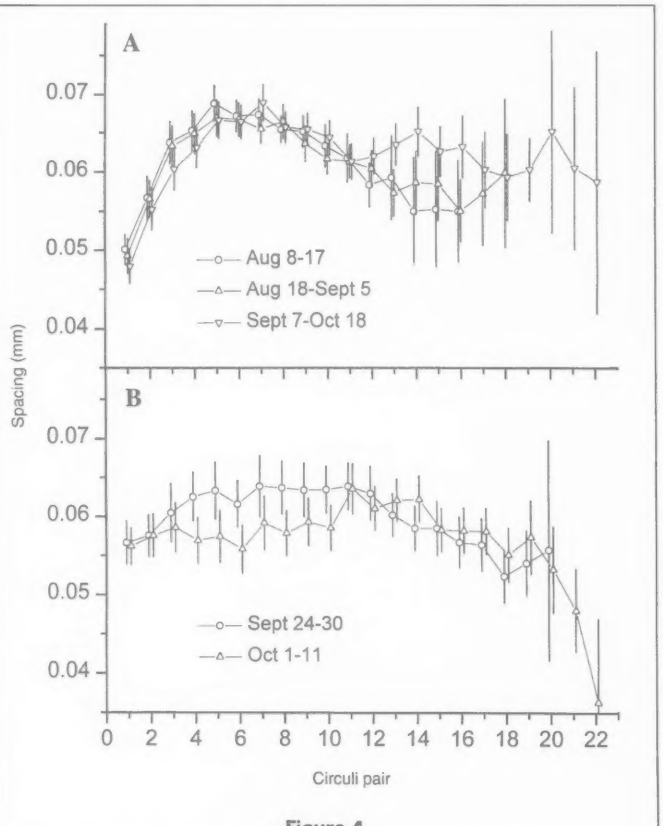


Figure 4

Circuli spacing versus circuli pair for Gulf of St. Lawrence postsmolts for two smolt year classes, 1982 (**A**) and 1983 (**B**). Samples are poststratified by date of capture. Error bars mark 95% confidence intervals.

In 1984, mean circuli spacing varied over a wide range, suggesting the different stocks experienced different growth regimes that year (Fig. 5C). What is particularly striking is that the wild-origin postsmolts from the Gulf had the narrowest mean spacings for most of the postsmolt growth season. Mean spacings for Gulf postsmolts were significantly lower than those for the comparison stocks with the exception of only one spacing pair (Table 4).

The three stocks provided for comparisons with Gulf of St. Lawrence postsmolts displayed a range of return rates and 1SW fraction, reflecting differences in survival and maturity rates. For the Connecticut stock, return rates of 2SW fish and 1SW fraction averaged 0.13% and 0.01, respectively (Table 5). Penobscot River smolts returned at higher rates, 0.09% and 0.47% for 1SW and 2SW fish, respectively. Typically 10% of the Penobscot cohort matured at 1SW. The Saint John stock had the highest return rates and the largest proportion of the cohort maturing after one-seawinter. The return rate for 1SW fish averaged 1.47% and the 1SW fraction averaged 0.59. The 2SW return rate for the Saint John stock is similar to that observed for the Penobscot stock. Thus, the Connecticut stock had the lowest survival rate and produced few early maturing fish; the Saint John stock had the highest survival rate and pro-

duced many early maturing fish; and the Penobscot stock was intermediate between the other two.

Discussion

Our analysis suggests that the role of the Gulf of St. Lawrence as salmon postsmolt nursery habitat varies annually. In some years it appears that the growth of wild postsmolts retained in the Gulf is as robust as and patterned similarly to growth observed for hatchery-origin postsmolts assumed to use open ocean habitats (Reddin and Short, 1991). This correlation suggests that either postsmolts from other areas invade the Gulf and use it as a nursery area or the Gulf region is continuous with a larger area of similar growth conditions where the nursery is formed. In other years, it appears that only smaller, and presumbably less robust, postsmolts remain in the Gulf area and that the nursery was formed elsewhere. Variation in the suitability of nursery habitat must interact with the ability of postsmolts to migrate successfully to more favorable areas. In what was first investigated as a mechanism controlling the return migration of adults, Groot and Cooke (1987) described an analogous situation with the distribution of juvenile sockeye salmon in the Strait of Georgia. It would appear that the dominant wind patterns in the Strait can alter the annual migration of postsmolt sockeye salmon and place them in different nursery areas each year (Peterman et al., 1994). Atlantic salmon postsmolt migration trajectories may be similarly affected. In some years, postsmolts are deposited in areas like the Gulf of St. Lawrence and growth conditions are favorable enough to retain them in the region for the entire season. In other years they are not deposited or retained in the same area. Regardless, our focus shifts to the factors controlling migration and whether they covary with the factors controlling survival.

We view nursery habitat for postsmolt salmon as being dynamically defined because it shifts spatial location on an annual basis to regions where the production will support growth. Many marine fishes use staged distribution separations between estuarine, coastal, and offshore habitats (Blabber et al., 1995). North American origin salmon are generally concentrated in the Labrador Sea as feeding adults or on various migration routes back to their natal rivers as maturing fish (Reddin and Shearer, 1987). However, postsmolt distributions are regulated in part by passive displacement mechanisms and the swim-

Table 3

Results of ANOVAs comparing scale circuli spacing for successive time periods from collections of postsmolt salmon from the Gulf of St. Lawrence during 1982 and 1983.

Year	Spacing pair	df effect	MS effect	df error	MS error	*F*	*P*-level	
1982	1	2	0.00015	369	0.00014	1.085	0.34	
	2	2	0.00008	369	0.00021	0.365	0.69	
	3	2	0.00036	369	0.00022	1.612	0.20	
	4	2	0.00013	369	0.00021	0.639	0.53	
	5	2	0.00021	369	0.00018	1.167	0.31	
	6	2	0.00002	369	0.00015	0.137	0.87	
	7	2	0.00038	368	0.00014	2.655	0.07	
	8	2	0.00003	368	0.00013	0.215	0.81	
	9	2	0.00017	355	0.00014	1.202	0.30	
	10	2	0.00027	324	0.00015	1.849	0.16	
1983	1	1	0.00001	152	0.00013	0.057	0.81	
	2	1	0.00000	152	0.00015	0.000	0.99	
	3	1	0.00014	152	0.00024	0.582	0.45	
	4	1	0.00120	152	0.00018	6.535	0.01	*
	5	1	0.00133	152	0.00024	5.424	0.02	*
	6	1	0.00129	152	0.00018	6.977	0.01	*
	7	1	0.00084	152	0.00027	3.067	0.08	
	8	1	0.00129	152	0.00019	6.713	0.01	*
	9	1	0.00064	152	0.00021	3.076	0.08	
	10	1	0.00093	152	0.00017	5.412	0.02	*

ming potential of the fish (Reddin and Friedland, 1993). As such, postsmolt migration routes are unlikely to be equivalent among years (Caron, 1983; Jonsson et al., 1993). At some point during the postsmolt's first growing season, swimming ability begins to exceed current velocity and postsmolts can more effectively modify their distribution according to preferences driven by migration mechanisms or foraging behavior. These factors may allow postsmolts to concentrate in specific habitats that best suit their feeding requirements and afford them some measure of protection from predation. However, the process of habitat selection may result in a nursery that encompasses different areas each year and thus not linked to a specific area (Friedland et al., 1996a). Therefore, years of poor feeding and growth conditions in the Gulf of St. Lawrence do not necessarily mean poor survival conditions because they do not preclude the use of other neritic areas as postsmolt nursery. For example, in some years the nursery may form along the south coast of Newfoundland or for that matter make use of few neritic habitats as the fish distribute in offshore areas.

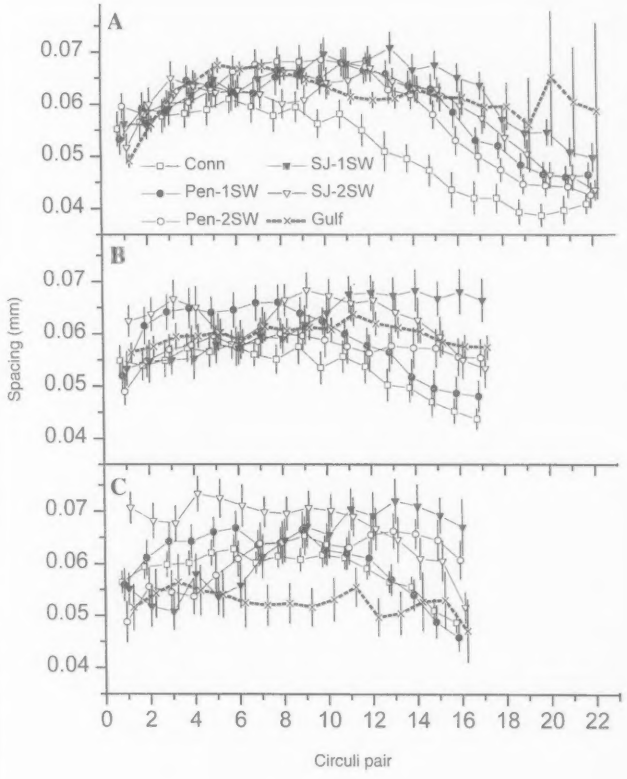


Figure 5

Circuli spacing versus circuli pair for Connecticut 2SW (Conn), Penobscot 1SW and 2SW (Pen), Saint John 1SW and 2SW (SJ), and Gulf of St. Lawrence postsmolts (Gulf) for three smolt year classes, 1982 (**A**), 1983 (**B**), and 1984 (**C**). Error bars mark 95% confidence intervals.

Contemporary characterizations of postsmolt populations may be inadequate if they fail to account for the distribution of postsmolts in neritic habitats. Coherence patterns in the performance of stock complexes has led investigators to search for broad-scale forcing functions to explain variation in returns rate by age (Friedland et al., 1993; Friedland et al., 1998a). In the Northeast Atlantic, a direct link between postsmolt survival and ocean climate has been reported (Friedland et al., 1998a). Spring thermal conditions were associated with the survival of North Sea stocks, which argues that the postsmolt nursery in that region was oceanic and thus directly affected by ocean climate change. However, interpretation of survival signals in the Northwest Atlantic has been complicated by the interplay of mortality and maturation (Friedland et al., 1998b). As the search continues for the factors affecting the survival of Northwest Atlantic postsmolts, investigators must be cognizant of the fact that much of the nursery may occur in inshore neritic waters rather than in pelagic ecosystems and thus may not respond solely to ocean-scale phenomena. This situation may be particularly important in evaluating coastal and offshore predators and how they might be impacting salmon populations. For example, a gannet colony may exert predation pressure over a substantial part of the northern coast of North America; thus, these and other bird species that are adapted to surface prey, such as Atlantic salmon postsmolts, could cause significant predation (Montevecchi and Myers, 1997).

The Gulf of St. Lawrence is a large, complex system that offers a diversity of feeding conditions to smolts upon their entrance into the marine environment. Growth rates would be expected to vary spatially in the Gulf owing to, among other things, highly variable thermal conditions over years. Nursery habitats within the Gulf appear to provide conditions that would support growth rates comparable to those observed in hatchery-reared stocks. But, what clearly differentiates the Gulf habitats from most offshore areas is the rapid continental cooling that occurs in the fall, resulting in an emigration of postsmolts from

Table 4

Results of ANOVAs comparing scale circuli spacing for Gulf of St. Lawrence postsmolts and 1SW and 2SW returns to the Connecticut, Penobscot, and St. John rivers for smolt years 1982–84.

Year	Spacing pair	df effect	MS effect	df error	MS error	*F*	*P*-level	
1982	1	1	0.00702	727	0.00015	47.053	0.000	*
	2	1	0.00057	727	0.00018	3.155	0.08	
	3	1	0.00086	727	0.00020	4.364	0.04	*
	4	1	0.00128	727	0.00018	7.165	0.01	*
	5	1	0.00425	727	0.00017	24.541	0.00	*
	6	1	0.00256	727	0.00015	16.600	0.00	*
	7	1	0.00248	726	0.00015	16.517	0.00	*
	8	1	0.00061	726	0.00015	4.086	0.04	*
	9	1	0.00001	713	0.00015	0.081	0.78	
	10	1	0.00081	682	0.00017	4.872	0.03	*
1983	1	1	0.00050	503	0.00016	3.117	0.08	
	2	1	0.00000	503	0.00019	0.004	0.95	
	3	1	0.00001	503	0.00021	0.029	0.87	
	4	1	0.00001	503	0.00023	0.032	0.86	
	5	1	0.00005	503	0.00022	0.232	0.63	
	6	1	0.00003	503	0.00020	0.156	0.69	
	7	1	0.00018	503	0.00021	0.873	0.35	
	8	1	0.00002	503	0.00018	0.093	0.76	
	9	1	0.00006	503	0.00020	0.277	0.60	
	10	1	0.00000	503	0.00020	0.002	0.97	
1984	1	1	0.00168	364	0.00018	9.118	0.00	*
	2	1	0.00125	364	0.00020	6.302	0.01	*
	3	1	0.00052	364	0.00022	2.396	0.12	
	4	1	0.00327	364	0.00020	11.568	0.00	*
	5	1	0.00336	363	0.00020	16.552	0.00	*
	6	1	0.00552	362	0.00022	25.136	0.00	*
	7	1	0.00551	362	0.00015	35.738	0.00	*
	8	1	0.00606	361	0.00016	39.032	0.00	*
	9	1	0.00783	360	0.00016	48.985	0.00	*
	10	1	0.00512	358	0.00017	31.024	0.00	*

Table 5

Percent return rate by age group and 1SW fraction for three hatchery index stocks. Return rates are in percent where fraction is proportion of cohort maturing after one sea-winter. Mean is for the period smolt years 1974–92.

Smolt year	Connecticut		Penobscot			St. John		
	2SW	Fraction	1SW	2SW	Fraction	1SW	2SW	Fraction
1982	0.02	0.00	0.05	0.52	0.08	0.91	0.65	0.49
1983	0.30	0.02	0.05	0.66	0.06	1.00	0.61	0.54
1984	0.09	0.00	0.04	0.59	0.04	0.98	0.39	0.59
Mean	0.13	0.01	0.09	0.47	0.12	1.47	0.57	0.59

the region (Dutil and Coutu, 1988). The northern Gulf can cool to temperatures below 2°C by late November and to lethal temperatures later in winter, from the surface to a depth of 100 m. Thus, the Gulf must be viewed as a seasonally transient habitat for postsmolts in most, if not all, years.

Our comparisons of growth patterns could be enhanced with the inclusion of growth information from stocks originating in the Gulf of St. Lawrence itself. We assumed that the range of growth patterns provided by the three comparison stocks is representative of stocks outside the Gulf region. However, the samples failed to account for growth signals from wild stocks and included only populations from the southern portion of the range. However, the strength of the sample is that it did include three stocks of varying growth and survival characteristics, thus supporting the contention that it likely represents a range of growth responses similar to those occurring in wild stocks.

A future challenge for research would be to characterize the thermal properties and production characteristics of the area potentially comprising the postsmolt nursery to evaluate its spatial and temporal extent and annual variability. From these descriptive analyses, it may be possible to design migration simulations and field experiments that could begin to describe the mechanisms that form the postsmolt nursery and, in turn, it may be possible to develop an understanding of the factors affecting postsmolt survival and recruitment in salmonid populations.

Acknowledgments

We thank L. Marshall, Department of Fisheries and Oceans, Halifax, for providing scale material from the Mactaquac Hatchery and summary return rate data, and J. Kocik and J. Boreman for reviewing early drafts of the manuscript.

Literature cited

Blabber, S. J. M., D. T. Brewer, and J. P. Salini.
1995. Fish communities and the nursery role of shallow inshore water of a tropical bay in the Gulf of Carpentaria, Australia. Estuarine Coastal Shelf Sci. 40(2):177–93.

Caron, F.
1983. Migration toward the Atlantic of postsmolt (*Salmo salar*) from the Gulf of St. Lawrence. Nat. Can. 110(2): 223–227.

Chadwick, E. M. P.
1985. The influence of spawning stock on production and yield of Atlantic salmon, *Salmo salar* L., in Canadian rivers. Aquacult. Fish. Manage. 16(1):111–719.
1987. Causes of variable recruitment in a small Atlantic salmon stock. Am. Fish. Soc. Symp. Ser. 1:390–401.

Chaput, G., J. Allard, F. Caron, J. B. Dempson, C. C. Mullins, and M. F. O'Connell.
1998. River-specific target spawning requirements for Atlantic salmon (*Salmo salar*) based on a generalized smolt production model. Can. J. Fish. Aquat. Sci. 55:246–61.

Cunjak, R. A., E. M. P. Chadwick, and M. Shears.
1989. Downstream movements and estuarine residence by Atlantic salmon parr (*Salmo salar*). Can. J. Fish. Aquat. Sci. 46(9):1466–1471.

Dutil, J.-D., and J.-M. Coutu.
1988. arly marine life of Atlantic salmon, *Salmo salar*, postsmolts in the northern Gulf of St. Lawrence. Fish. Bull. 86(2):197–212.

Elliott, J. M.
1993. A 25-year study of production of juvenile sea-trout, *Salmo trutta*, in an English Lake District stream. Can. Spec. Publ. Fish. Aquat. Sci. 118:109–22.

Eriksson, T.
1994. Mortality risks of Baltic salmon during downstream migration and early sea-phase: effects of body size and season. Nord. J. Freshwater Res. 69:100.

Friedland, K. D., D. W. Ahrenholz, and J. F. Guthrie.
1996a. Formation and seasonal evolution of Atlantic menhaden juvenile nurseries in coastal estuaries. Estuaries 19(1):105–114.

Friedland, K. D., R. E. Haas, and T. F. Sheehan.
1996b. Postsmolt growth, maturation, and survival of two stocks of Atlantic salmon. Fish. Bull. 94(4):654–63.

Friedland, K. D., L. P. Hansen, and D. A. Dunkley.
1998a. Marine temperatures experienced by postsmolts and the survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. Fish. Oceanogr. 7:22–34.

Friedland, K. D., D. G. Reddin, and J. F. Kocik.
1993. Marine survival of North American and European Atlantic salmon: effects of growth and environment. ICES J. Mar. Sci. 50:481–92.

Friedland, K. D., D. G. Reddin, N. Shimizu, R. E. Haas, and A. F. Youngson.
1998b. Strontium:calcium ratios in Atlantic salmon otoliths and observations on growth and maturation. Can. J. Fish. Aquat. Sci. 55:1158–1168.

Groot, C., and K. Cooke.
1987. Are the migrations of juvenile and adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in near-shore waters related? Can. Spec. Publ. Fish. Aquat. Sci. 96: 53–60.

Holm, M., J. Holst, and L. Hansen.
1996. Atlantic salmon surveys in the Norwegian Sea from July 1991–August 1995. Aquaculture 1996(1):21.

Jonsson, N., L. P. Hansen, and B. Jonsson.
1993. Migratory behavior and growth of hatchery-reared postsmolt Atlantic salmon *Salmo salar*. J. Fish Biol. 42:435–443.

Kuikka, S., and M. Salminen.
1994. Dependency of stocking result on the size of the released salmon smolts (*Salmo salar* L.) in the northern part of the Baltic Sea. Nord. J. Freshwater Res. 69:99.

Larsson, P.-O.
1985. Predation on migrating smolt as a regulating factor in Baltic salmon, *Salmo salar* L., populations. J. Fish Biol. 26(4):391–397.

Levings, C. D.
1994. Feeding behavior of juvenile salmon and significance of habitat during estuary and early sea phase. Nord. J. Freshwater Res. 69:7–16.

Montevecchi, W. A., D. K. Cairns, and V. L. Birt.
1988. Migration of postsmolt Atlantic salmon, *Salmo salar*, off northeastern Newfoundland, as inferred by tag recoveries in a seabird colony. Can. J. Fish. Aquat. Sci. 45(3): 568–71.

Montevecchi, W. A., and R. A. Myers.
1997. Centurial and decadal oceanographic influences on changes in northern gannet populations and diets in the north-eest Atlantic: implications for climate change. ICES Journal of Marine Science 54:608–14.

Peterman, R. M., S. G. Marinone, K. A. Thomson, I. D. Jardine, R. N. Crittenden, P. H. Leblond, and C. J. Walters.
1994. Simulation of juvenile sockeye salmon (*Oncorhynchus nerka*) migrations in the Strait of Georgia, British Columbia. Fish. Oceanogr. 3(4):221–35.

Reddin, D. G., and K. D. Friedland.
1993. Marine environmental factors influencing the movement and survival of Atlantic salmon. *In* D. Mills (ed.), salmon in the sea, p. 79–193. Fishing News Books, London.

Reddin, D. G., and W. M. Shearer.
1987. Sea-surface temperature and distribution of Atlantic salmon in the Northwest Atlantic Ocean. Am. Fish. Soc. Symp. Ser. 1:262–75.

Reddin, D. G., and P. B. Short.
1991. Postsmolt Atlantic salmon (*Salmo salar*) in the Labrador Sea. Can. J. Fish. Aquat. Sci. 48(1):2–6.

Robitaille, J. A., Y. Cote, G. Shooner, and G. Hayeur.
1986. Growth and maturation patterns of Atlantic salmon, *Salmo salar*, in the Koksoak River, Ungava, Quebec. *In* D. J. Meerburg (ed.), Salmonid age at maturity, p. 62–69. Can. Spec. Publ. Fish. Aquat. Sci. 89.

Shelton, R. G. J., W. R. Turrrell, A. MacDonald, I. S. McLaren, and N. T. Nocoll.
1997. Records of postsmolt Atlantic salmon, *Salmo salar* L., in the Faroe-Shetland Channel in June 1996. Fisheries Research (Amsterdam) 31(1–2):159–62.

Thorpe, J.
1994. Salmonid fishes and the estuarine environment. Aquaculture 17(1A):76–93.

A new method for indexing spawning stock and recruitment in ocean shrimp, *Pandalus jordani*, and preliminary evidence for a stock-recruitment relationship

Robert W. Hannah
Oregon Department of Fish and Wildlife
Marine Program
2040 S.E. Marine Science Drive
Newport, Oregon 97365
E-mail address: bob.hannah@hmsc.orst.edu

Abstract.—Using improved indices of age-1 recruitment and parent stock, I investigated the existence of a stock-recruitment relationship for ocean shrimp, *Pandalus jordani*. I also examined the effects of large catches of egg-bearing shrimp in April on subsequent recruitment. After known environmental influences were accounted for, regression analysis revealed evidence of a quasilinear relationship between recruitment and either spawning stock or egg production. The stock-recruitment relationship showed that average recruitment increases if higher spawner abundance is maintained in years of low abundance. The recruitment-stock relationship, however, showed that low abundance of spawning fish was mostly a result of environmentally driven recruitment failures, rather than just fishery impacts. Fishing did contribute to the low numbers of spawning fish in 1993, and catches of egg-bearing shrimp in April 1989 may have also depressed the 1990 year class. The strong recruitment-stock relationship for ocean shrimp suggests that an increase in escapement of all ages of shrimp in response to a year-class failure may do more to bolster recruitment than traditional strategies aimed at protecting age-1 shrimp.

Manuscript accepted 11August 1998.
Fish. Bull. 97:482-494 (1999).

Recruitment of the ocean shrimp, *Pandalus jordani*, to the fishery in waters off Oregon has been shown to be influenced strongly by ocean conditions during early larval stages (Hannah, 1993). Specifically, sea level height (SLH) during the month of April, shortly after the bulk of larval release, is strongly negatively correlated with recruitment of age-1 shrimp to the fishery the following year (Hannah, 1993). Although the mechanism linking recruitment to April SLH remains unclear, April SLH probably integrates the strength and timing of the spring transition in coastal currents (Huyer et al., 1979). Ocean shrimp larvae inhabit the near-surface waters shortly after release, occupying progressively deeper strata as they develop (Rothlisberg, 1975; Rothlisberg and Miller, 1983). The nature of the spring transition probably influences the alongshore transport of early larvae, as well as the nearshore temperature regime, either of which could strongly influence shrimp larval survival (Rothlisberg, 1975; Rothlisberg and Miller, 1983; Hannah, 1993; McConnaughey et al., 1994).

Attempts to relate ocean shrimp recruitment to the size of the parent spawning stock, even allowing for the influence of April SLH, have been unsuccessful (Abramson and Tomlinson, 1972; Gotshall, 1972; Geibel and Heimann, 1976; Hannah, 1993). Efforts to date have, to a large degree, relied on assumptions of constant catchability and natural mortality. Recently, both natural mortality rates and the catchability coefficient have been shown to be quite variable for ocean shrimp (Hannah, 1995). I have suggested previously that variation in catchability and natural mortality may have created large enough errors in prior indices of shrimp stock and recruitment as to obscure an underlying relationship between these two variables (Hannah, 1995). In the present study, new indices of ocean shrimp recruitment and spawning stock were developed which do not rely, or rely only very minimally, on assumptions of constant catchability and natural mortality. The main objective of this study was to re-examine the relationship between shrimp recruitment and both shrimp spawning stock and April SLH in the year of larval release, using these improved indices.

Another problem with earlier studies of ocean shrimp stock size and recruitment is that they have relied on measures of parent stock or spawning biomass, rather than on more direct measures of reproductive output, such as estimates of

egg production (Rothschild and Fogarty, 1989; Hannah et al., 1995). A second objective of this study was to construct, in addition to an improved index of spawning stock, an index of egg production, and evaluate the relationship between recruitment and egg production. One of several challenges in constructing such an index is that the trawl fishery harvests egg-bearing female shrimp in late October, just before the fishing season ends, and again in early April, as fishing resumes. It can be argued that because of reduced fishing effort late in the season in most years and because of the high natural mortality rates experienced by ocean shrimp over the winter, the harvest of egg-bearing shrimp in October should have a negligible impact on total larval release the next spring. However, in April, when larval release is imminent for any shrimp still bearing eggs, the impact of the fishery could be more detrimental. Also, with much of the larval release taking place before the fishing season opens on 1 April, fishery impacts are concentrated on late-release larvae. If, as postulated in the prior study (Hannah, 1993), the timing of the spring transition is critical to larval survival or retention in the study area, the fishery may be impacting the larvae with the greatest chances for success in a poor environment: those destined for release after a late spring transition. A third objective of this study was to estimate the harvest of egg-bearing shrimp in April and examine the impact that April harvest of egg-bearing shrimp may have had on subsequent recruitment.

Materials and methods

In my earlier study of ocean shrimp stock and recruitment (Hannah, 1993), I used an age-structured index of recruitment calculated by summing two components. The first component was an estimate of the age-2 shrimp population in April (year t), calculated from the average fishery catch per unit of effort (CPUE) of age-2 shrimp in April and May, divided by an assumed catchability coefficient calculated from data in Geibel and Heimann (1976). The second component was simply a sum of the catch of age-1 shrimp during the prior year (t–1), with each monthly catch discounted to 1 April of year t by using an assumed monthly natural mortality rate of 0.096 (Gotshall, 1972). In essence, this index was a crude estimate of what the age-2 shrimp population would have been in the absence of fishing, on 1 April of the age-2 year (Hannah, 1993). To index the shrimp spawning stock in the earlier study, I used a simple average of September–October shrimp fishery CPUE. Both indices depended heavily on an assumption of constant catchability. The recruitment index also relied on an assumption of constant natural mortality.

The relationship between CPUE, population size, geographic stock area, and the catchability coefficient can be described by the equations

$$CPUE = paNA^{-b} \quad (1)$$

$$q = paA^{-b}, \quad (2)$$

where p = the proportion of shrimp within the sweep of the gear that will be captured (the elemental efficiency);
A = the geographic stock area (stock area);
a = the area covered by a single sweep of the gear;
b = a coefficient that describes how q will vary with stock area;
N = the population size; and
q = the catchability coefficient (Winters and Wheeler, 1985).

Accordingly, an assumption of constant catchability is equivalent to assuming that stock area is constant. However, stock area for ocean shrimp has been shown to be roughly proportional to stock abundance and to vary substantially between years (Hannah, 1995; Hannah, 1997). In the present study, I incorporated stock area estimates into both the shrimp recruitment and spawner indices, making an assumption of constant catchability unnecessary. I did assume that b in the above equation was equal to 1, an assumption that has been previously shown to be reasonable, according to a roughly linear relationship between stock area and abundance (Hannah, 1995). My approach also assumes that the elemental efficiency of shrimp trawl gear, p, is constant.

Because the assumed rate of natural mortality was used in the prior study (Hannah, 1993) only to discount age-1 catches forward in time to 1 April of the age-2 year, the simplest way to reduce the influence of variable natural mortality on the recruitment index is to index the population at an earlier age. This is a useful approach; however, age-1 shrimp must still be fully recruited to the fishery at the time chosen. Using data from the early years of the shrimp fishery, Lo (1978) showed that age-1 shrimp were incompletely recruited to the California shrimp fishery, especially early in the April–October season. A variety of data suggest that, since about 1979, age-1 shrimp have been fully recruited to the trawl fishery by June or July of each year. Prior to 1974, Oregon required a minimum codend mesh of 34.9-mm (1 3/8 in) stretch measure. Since this date, minimum codend mesh size has been unregulated in the Or-

egon fishery, although California still requires a minimum codend mesh of 34.9 mm. Prior to 1978, shrimp growth was slower (Hannah and Jones, 1991) and age-1 shrimp in the study area (Fig. 1) were clearly not fully recruited to trawl gear until very late in the season (ODFW[1]). After 1978, shrimp growth increased, possibly owing to reduced density from heavy fishing, although other factors were also involved, notably accelerated sex change that may have been a response to reduced numbers of older shrimp (Charnov et al., 1978; Hannah and Jones, 1991). Average codend mesh size in the Oregon fleet also decreased sometime during the 1970s, averaging 30.2 mm by 1981, decreasing to 28.7 mm by 1991–92 (Jones et al., 1996). Accordingly, in this study I chose the August–September time period to index the age-1 shrimp population, and restricted my analysis to the years after 1979. With the months of August–September, the population was indexed eight months earlier than in the previous study, but at a time period late enough that age-1 shrimp could reasonably be assumed to be fully recruited to the trawl gear being fished.

To index shrimp recruitment in the present study, I used the average August–September CPUE for age-1 shrimp only as an index of density and multiplied this index by stock area (ha) for the same year class (Hannah, 1997). In this case, CPUE was expressed as shrimp per hectare trawled, using an average estimate of 5.93 ha trawled per single-rig equivalent hour fished (Hannah, 1995). To account for years in which early season catches of age-1 shrimp were high, I added in the catch of age-1 shrimp for the months of April–July of the same year. Thus, recruitment was calculated as

$$R_t = (D_t A_t) + C_t, \quad (3)$$

where R = recruitment of age-1 shrimp in year t;
D = the average fishery CPUE of age-1 shrimp in August and September of year t;
A = the stock area for the age-1 year class in year t; and
C = the summed fishery catch of age-1 shrimp in the months April to July of year t.

Use of these additional catches for April–July does rely on an assumption of constant natural mortality, although the importance of this assumption is clearly reduced. Age-1 shrimp CPUE for Pacific States Marine Fisheries Commission (PSMFC) statistical areas 82–88 was obtained from Zirges et al. (1982) and Hannah et al. (1997). The collection and analysis of biological samples from the commercial catch has been described by Hannah and Jones (1991).

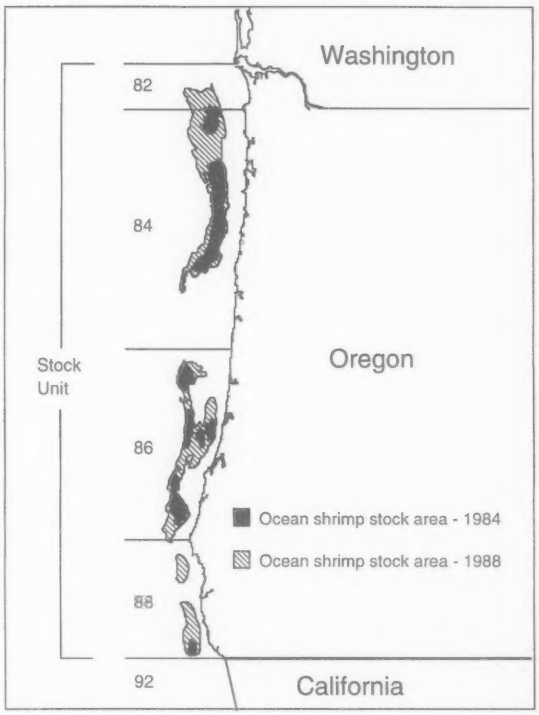


Figure 1

Location of commercial concentrations of ocean shrimp (*Pandalus jordani*) off coastal Oregon, in Pacific States Marine Fisheries Commission statistical areas 82–88. Dark areas show the approximate minimum areal extent of the shrimp grounds (1984) and the lighter shaded areas show the largest areal extent observed from 1980 to 96 (1988).

The data used to construct the recruitment and spawning stock indices developed in this study differ in some respects from the data used for the prior recruitment study. In the prior study, logbook data were available from Washington, Oregon, and California, such that a complete accounting of catch and effort was possible for PSMFC areas 82–92 (Fig. 1). Beginning in 1992, logbook data from the states of California and Washington became unavailable. Accordingly, the data used in this study was based on Oregon landings for the entire study period. To minimize the impact of the missing information on the indices developed, the study area was limited to areas 82–88 (Fig. 1). I believe that the missing information will create very minimal error in the new indices for several reasons. First, Oregon landings comprise the great majority of the removals of shrimp from statistical areas 82–88. The average percent-

[1] ODFW (Oregon Department of Fish and Wildlife). 1981 to present. 2040 SE Marine Science Dr., Newport, OR. Unpubl. data.

age of total catch from these areas landed in Oregon from 1980 to 1992 was 92.5% (Hannah et al., 1997). Second, the components of the new indices, with one exception, did not depend on a complete accounting of catch and effort from the study area but simply on a good estimate of average CPUE at age and accurate estimates of stock area. The one component of the recruitment index that was somewhat influenced by the missing catch data was the added age-1 shrimp catch from the months of April–July. A correction for this potential source of error is not available; however, I believe the magnitude of error introduced is likely to be small in relation to the interannual variation in the index itself.The use of CPUE as a direct index of density is equivalent to assuming that elemental efficiency, p in Equation 2 above, equals 100%. This is clearly not reasonable, however; selecting a value for p is problematic. The principal importance of selecting a value for p is to obtain a proper scaling between the two components of the recruitment index: one based on CPUE and stock area; the other based on the early-season catch of age-1 shrimp. Proper scaling of these two components is less critical than it seems at first examination because the two index components are actually closely correlated (r=0.774 at p=0.5). Accordingly, a change in the scaling between the two components is expected to have little influence on the pattern of time series variation in the resulting index. As a check on this assumption, all indices using CPUE as a density index in this study were calculated with a range of p-values, and the results were then examined to see if they were sensitive to assumptions about p. For the primary analysis, I chose a p-value of 0.5 and for the sensitivity analysis I used values of 0.25 and 0.75. for p, following my earlier examination of shrimp mortality rates (Hannah, 1995).

Commercial logbook data were used to generate estimates of stock area for each shrimp year class. The methods used to estimate stock area, including the correction of estimates for variation in sampling rates, are described in detail in Hannah (1997). Stock area was estimated by using logbook data from June of the recruit year through May of the following year, the time period during which age-1 shrimp contribute most heavily and reliably to the catch. For a few of the years in the 1980–96 time series, the fishery failed to target age-1 shrimp adequately, and harvested primarily the remaining age-2 and older shrimp from prior year classes. For those years, stock area was estimated from a linear regression of stock area on a simple virtual population estimate for that year class, as described in Hannah (1997).

To index the ocean shrimp spawning stock, I used an approach similar to that used for the recruitment index. For each spawning year, I used the average age-specific CPUE in September–October as an index of age-specific density. Once again, these estimates of density were expanded by using assumed levels of elemental trawl efficiency ranging from 0.25 to 0.75, as discussed above. I then multiplied each density index by the stock-area estimate for that year class, as calculated in the year of recruitment. In using this approach I assumed that the geographic distribution of each newly recruited year class was established at settlement and was persistent, and that local shrimp density was modified by fishing and natural mortality. This assumption is supported by several observations, including the obvious autocorrelation in stock area estimates noted previously (Hannah, 1995), the lack of any evidence for migration in this species and the approximately linear relationship between stock area and abundance. There is some evidence from sea bed drifter recoveries (ODFW[1]) that suggests slow gyres in bottom currents may help retain or concentrate shrimp in some of the major shrimp beds. However, it is unknown whether this effect is sufficiently large to actually alter the areal extent of a shrimp year class after settlement.

An egg production index for ocean shrimp was calculated by expanding the spawner index with available shrimp biological data (ODFW[1]). The biological data used included the mean percentage of females and mean female shrimp carapace length, by age, from samples of the fishery in October. For a few years, October samples were unavailable and September samples were used. I used a pooled length-fecundity relationship from Hannah et al. (1995) to estimate mean fecundity for each age group of female shrimp based on mean carapace length data.

The April harvest of egg-bearing females was estimated for the years 1979–95 in a straightforward manner. April shrimp catch, expressed as numbers of shrimp, for each PSMFC statistical area, was obtained from Hannah et al. (1997). Catch in numbers was multiplied by the average percentage of egg-bearing shrimp estimated for each PSMFC area from biological samples of the April catch (ODFW[1]). The catch of egg-bearing shrimp from each of the four areas (Fig. 1) was then summed.

Because the percentage of egg-bearing shrimp declined throughout April, a time-stratified approach was used to estimate the average percentage of egg-bearing shrimp. One problem with this approach is variation in sample coverage. Although the total number of shrimp examined from the April catch has been fairly consistent, averaging about 2900 shrimp from 1980 to 1996, the early and late portions of April have not always been sampled evenly. For example, some years that had excellent sample coverage in

the first two weeks of April had no samples at all for the second half of the month. To make maximum use of the data available, estimates of the percentage of egg-bearing shrimp from individual samples were averaged for the first and second halves of the month, respectively. These semimonthly figures were then averaged to produce an overall mean percentage of egg-bearing shrimp in the catch for each April. When samples were missing from the latter half of the month, a zero level of ovigerous shrimp was assumed. When samples were missing for the first half of the month, the level of ovigerous shrimp observed for the second half was assumed as a minimum estimate for the first half of April. Accordingly, the estimates presented in the present study are minimum estimates of the catch of egg-bearing shrimp.

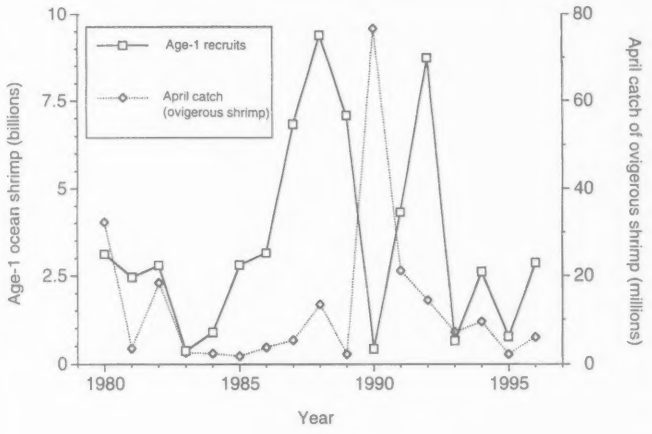


Figure 2

Time series of the recruitment index, calculated assuming elemental trawl efficiency of 0.50, and the fishery catch of egg-bearing shrimp from April of the year of larval release, by year of age-1 recruitment, 1980–96.

To determine when, during the month of April, egg-bearing shrimp had declined to a minimal component of the catch, I constructed a scatter graph of the raw percentages of egg-bearing females by date, using existing data for 1961–97 (ODFW[1]). Area 82 (Fig. 1) was excluded from this analysis because the incidence of egg-bearing shrimp in this area was generally very low in April.

A stepwise process was used to evaluate the relationships between the new recruitment, spawner, and egg production indices, calculated at assumed values of 0.25., 0.50 and 0.75 for trawl efficiency. Following the findings of my earlier study (Hannah, 1993), the first step in this analysis was to regress log (natural log unless noted) recruitment against April SLH at Crescent City, California, to verify that SLH still explained a significant amount of the interannual variation in recruitment. Simple linear regression was used for this test. These SLH data were obtained from the National Oceanic and Atmospheric Administration's Ocean and Lake Levels Division for the years 1979–95, corresponding to age-1 catch years 1980–96. Next, the residuals were examined and compared graphically and by means of linear regression to the spawner and egg production indices, and outliers were examined in light of the estimates of the catch of egg-bearing shrimp in April. Finally, some multivariate models incorporating April SLH and the spawner and egg production indices were fitted by using multiple regression.

Garcia (1983) and others have stressed that many of the stock-recruitment relationships that have been demonstrated for shrimp stocks are really statistical artifacts caused by a strong recruitment-stock relationship (the reverse of a stock-recruitment relationship, rather spawning stock in year t as a function of recruitment that same year) in combination with serially autocorrelated, environmentally driven, recruitment. To test for such a possibility in the present analysis of ocean shrimp recruitment, I regressed the new recruitment index against itself at a lag of one year. I also examined the recruitment-stock relationship further by graphically comparing the spawning index, broken out by age class, to the recruitment index from the same year.

Results

The recruitment index (Fig. 2; Table 1; all indices calculated assuming 0.50 for trawl efficiency, unless noted) shows wide variation in ocean shrimp recruitment, especially after 1986 (year of age-1 recruitment, unless noted). Recruitment in 1983, 1984, 1990, and 1993 was very low, whereas very high recruitment was observed for the 1987–89 and 1992 year classes. These four large year classes had a very significant influence on total landings from the shrimp fishery during the years included in this study. Although they represent less than one third of the years in the time series, they contributed roughly 60% of the total landings of shrimp.

The log of the shrimp recruitment index was stongly negatively correlated with April SLH at Crescent City, California, in the year of larval release

Table 1

Ocean shrimp population data used for regression analyses, including April SLH, geographic stock area (year is June–May), and recruitment, spawner, and egg production indices, by calendar year (no lags). Recruitment, spawner, and egg production indices are calculated assuming elemental trawl efficiency of 0.50.

Year	Recruitment index (millions — age 1)	April SLH (cm)	Geographic stock area (1000 ha)	Spawning abundance (millions)	Egg production (billions)
1979	—	214.9	—	—	—
1980	3122.0	218.2	450.6	—	—
1981	2455.0	210.9	477.2	—	—
1982	2789.1	226.5	344.1	2133.0	2002.9
1983	368.6	229.2	172.9	604.0	717.1
1984	884.5	211.5	158.7	1150.7	1257.4
1985	2798.4	213.1	319.4	3049.7	1913.4
1986	3148.7	212.5	460.5	2293.1	1616.0
1987	6840.2	209.1	464.6	3760.3	2558.0
1988	9388.1	214.9	605.0	7332.6	5783.8
1989	7078.9	222.2	585.1	6872.6	4845.5
1990	429.2	219.2	208.8	1652.2	3583.3
1991	4312.5	212.5	478.1	2141.4	1590.4
1992	8729.9	230.7	406.3	4519.7	4146.1
1993	649.9	227.4	200.8	921.4	1670.2
1994	2608.4	215.0	364.1	1465.3	1291.0
1995	768.6	220.0	215.7	—	—
1996	2862.8	—	362.0	—	—

(Fig. 3). The linear regression model (Table 2; model 1) was highly significant, with April SLH explaining 48% (unadjusted for degrees of freedom, unless noted) of the variation in log recruits. More importantly, the linear relationship is not based heavily on just a few points but appears quite general in nature, confirming a routine relationship between recruitment and April SLH shortly after the peak of larval release.

The residuals from the regression of log recruits on April SLH, graphed against the spawner index, show a pattern that is suggestive of a quasilinear stock-recruitment relationship, with the 1990 year class as an exceptional outlier (Fig. 4). The same residuals regressed against the egg production index show a similar pattern (Fig. 5). The time series of recruitment and the April catch of egg-bearing shrimp from the year of larval release (Fig. 2) shows that the year class released in 1989 (1990 year class) may have been heavily impacted by the trawl fishery, owing to an extremely high harvest of late egg-bearing shrimp. This occurred in combination with a high April sea level, suggestive of a late spring transition (Table 1). Data on the percentage of ovigerous females in the April catch (Fig. 6) suggest that postponement of the opening of the season to April 20th each year could eliminate this impact.

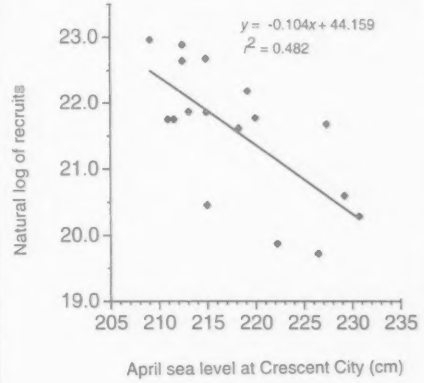


Figure 3

Linear regression of the natural log of the shrimp recruitment index, calculated assuming elemental trawl efficiency of 0.50, versus mean sea level height at Crescent City, California, during April of the year of larval release.

When the 1990 year class was excluded, neither scatter graph (Figs. 4–5) exhibited sufficient evidence of curvature to indicate the most appropriate form

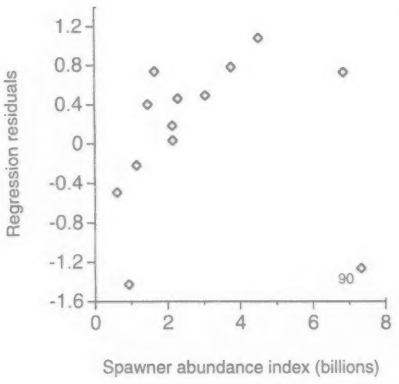


Figure 4

Residuals from regression of ln(recruits) on April SLH at Crescent City, California, versus the ocean shrimp spawner index from the parent year. Both indices were calculated assuming elemental trawl efficiency of 0.50.

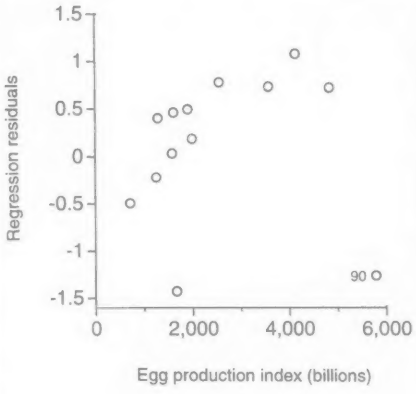


Figure 5

Residuals from the regression of ln(recruits) on April mean sea level height at Crescent City, California, versus the ocean shrimp egg production index from the parent year. Both indices were calculated assuming elemental trawl efficiency of 0.50.

of the stock-recruitment relationship for ocean shrimp. If the 1990 year class was included, the graphs could be interpreted as supporting a dome-shaped stock-recruitment curve, or could even be interpreted as evidence of no relationship between stock and recruitment at all. Given the extremely large fishery impact on egg-bearing females in the spring of 1989 (Fig 2), in combination with the fact that April has been shown to be a critical period for larval survival, excluding the 1990 data point seems the most conservative approach. With the 1990 year class excluded, a multivariate model incorporating April SLH and the log of the spawner index, was highly significant ($P<0.001$) and explained 79% of the variation in log recruitment (Table 2, model 2). The comparable multivariate model, incorporating the egg production index, was also highly significant ($P<0.01$) and explained 68% of the variation in log recruitment (Table 2, model 3). Both models incorporated April SLH and log spawners or eggs with negative and positive slopes, respectively. A linear regression of the recruitment index on itself, at a lag of one year, was nonsignificant ($P>0.05$) and showed little evidence of serial autocorrelation, suggesting that the evidence presented in Figures 4 and 5, for a statistical dependence of recruitment on parent stock in ocean shrimp, may be valid.

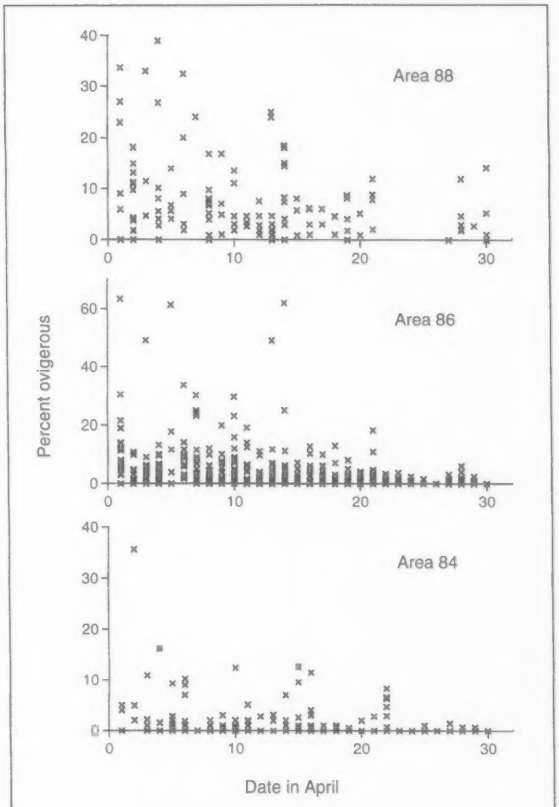


Figure 6

The percentage of egg-bearing shrimp in April samples of the ocean shrimp fishery, for Pacific States Marine Fisheries Commission areas 84–88, 1961–97.

Table 2

Results of univariate and multivariate regression analysis. Dependent variable is the natural log of the ocean shrimp recruitment index in year t. All population indices are calculated assuming elemental trawl efficiency of 0.50.

Parameters and variables	Coefficients	95% CI	F-value	R^2 (adjusted)	$P>F$
Model 1					
Intercept	44.159				
April SLH_{t-1}	−0.104	±0.059			
Full Model			13.983	0.448	0.0020
Model 2 (1990 excluded)					
Intercept	29.108				
April SLH_{t-1}	−0.112	±0.047	29.388		0.0004
Ln (spawner index)$_{t-2}$	0.796	±0.502	12.893		0.0058
Full Model			16.550	0.739	0.0010
Model 3 (1990 excluded)					
Intercept	21.636				
April SLH_{t-1}	−0.103	±0.056	17.528		0.0024
Ln(egg index)$_{t-2}$	0.799	±0.754	5.743		0.0401
Full Model			9.676	0.612	0.0057
Model 4					
Intercept	27.531				
April SLH_{t-1}	−0.119	±0.053	26.037		0.0006
Ln(spawner index)$_{t-2}$	0.957	±0.628	11.879		0.0073
April catch of ovigerous Shrimp$_{t-1}$ (millions)	−0.035	±0.022	13.006		0.0057
Full model			11.956	0.733	0.0017

A multivariate model, using the complete data series and incorporating April SLH, the natural logarithm of the spawner index, and the April catch of egg-bearing shrimp from the year of larval release, was also highly significant ($P<0.005$) and explained 80% of the variation in log recruitment (Table 2, model 4). As expected, the coefficients for SLH and the catch of egg-bearing shrimp in April of the release year were both negative, whereas the coefficient for the natural logarithm of spawners was positive. Fitting this three-variable model, with the 1990 year class excluded, resulted in the catch of egg-bearing shrimp not contributing significantly to the overall model fit, suggesting that this variable does not have general predictive value for the recruitment time series but is useful only in explaining the very low recruitment in 1990.

Despite efforts to de-emphasize the importance of age-1 catches in the recruitment series by indexing the stock at an earlier age, these early catches still represented a large component of the index (Fig. 7). This finding suggests that the assumption of constant natural mortality could still be inducing errors in the recruitment index. However, when the analyses discussed above were conducted on the recruitment index excluding the April–July age-1 catches, the results were very similar. This similarity argues that the findings of this study are not sensitive to failure of the assumption of constant natural mortality, as it is employed in calculating the recruitment index. The results were also insensitive to the assumed level of elemental trawl efficiency (Table 3, models 5 and 6).

The data in Figure 4 suggest that if shrimp spawner abundance could be maintained above some threshold (about 1.3 billion shrimp for an assumption of 0.50 for elemental trawl efficiency), the ability to produce large shrimp year classes in favorable environmental conditions could be preserved in all years. A similar threshold could also be identified in terms of egg production (Fig. 5). Examination of the relationship between age-1 spawners, older spawners, and the recruitment index from the same calendar year (Fig. 8), suggests a strong recruitment-stock relationship for ocean shrimp and a minor role for the fishery in determining spawner abundance. In

Table 3

Results of multivariate regression analysis using alternative assumed values for elemental trawl efficiency. Dependent variable for models 5 and 6 is the natural log of the ocean shrimp recruitment index in year t, calculated assuming elemental trawl efficiency of 0.25 and 0.75, respectively.

Parameters and variables	Coefficients	95% CI	F-value	R^2 (adjusted)	$P>F$
Model 5 efficiency of 0.25					
Intercept	27.583				
April SLH_{t-1}	−0.122	±0.056	24.306		0.0008
Ln (spawner index)$_{t-2}$	0.976	±0.666	11.022		0.0089
April catch of ovigerous Shrimp$_{t-1}$ (millions)	−0.038	±0.024	13.252		0.0054
Full model			11.500	0.724	0.0020
Model 6 efficiency of 0.75					
Intercept	27.437				
April SLH_{t-1}	−0.117	±0.051	26.829		0.0006
Ln (spawner index)$_{t-2}$	0.946	±0.608	12.378		0.0065
April catch of ovigerous Shrimp$_{t-1}$ (millions)	−0.034	±0.022	12.683		0.0061
Full model			12.107	0.735	0.0016

each of the years in which spawner abundance falls below the proposed threshold, there was a serious recruitment failure, depressing the age-1 population. In the case of spawn-year 1984, two year-class failures in a row were evident. All of the very low year classes shown in Figure 8 coincide with high April SLH the prior year (Table 1), suggesting that most low spawner abundances were largely the result of environmental forcing and a strong recruitment-stock relationship. Two of the years shown, 1984 and 1993, followed the major El Niño southern oscillation (ENSO) events of 1982–83 and 1992–93, and likely resulted from the rise in sea levels and accelerated northward currents often associated with these events and their likely influence on conditions in April (Huyer et al., 1979; Chelton and Davis, 1982; Chelton et al., 1982; Huyer and Smith, 1985).

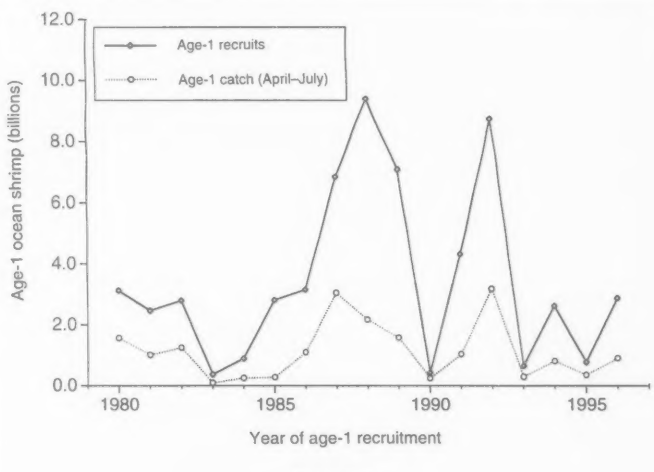


Figure 7

Age-1 ocean shrimp recruitment index, calculated assuming elemental trawl efficiency of 0.50, and the portion of the index for the April–July catch of age-1 shrimp, by year, 1980–96.

However, the data suggest that the fishery does play some role in creating the low spawner abundances shown in Figure 8. Although the low recruitment in 1990 corresponds to a poor spring transition in 1989 (Table 1), the data suggest that the high harvest of egg-bearing females in April of 1989 exacerbated this recruitment failure (Fig. 2; Tables 1 and 2), subsequently depressing spawner abundance (Fig. 8). The large difference between age-1 recruitment and the age-1 component of the spawner index in 1993 (Fig. 8) also suggests that spawner abundance may have been depressed by the fishery in that year. The close association between a year-class failure and low spawning abundance the same year also demon-

strates that attempting to maintain a spawner threshold by increasing escapement of age-1 shrimp is unlikely to be an effective management strategy. The reason for this is that precisely when a boost in spawner abundance is needed, the age-1 year class is too depressed to offer significant help, even with a complete cessation of fishing. This result suggests that when a year-class failure is detected in this stock, reducing fishery impacts on all age classes of shrimp may be a better strategy to maintain spawner abundance than the standard management measures (e.g. mimimum codend mesh or maximum count per pound) which protect the escapement of age-1 shrimp.

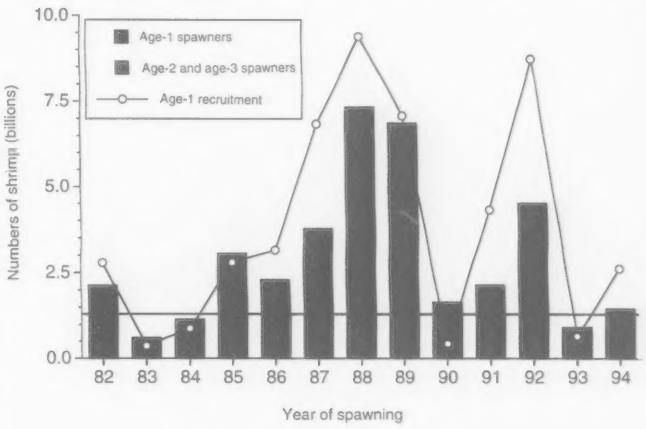


Figure 8

Ocean shrimp spawner index, broken down by age, and age-1 recruitment index for the same year, 1982–94. All data are calculated assuming elemental trawl efficiency of 0.50. Horizontal line indicates a hypothetical management threshold for spawner abundance.

Discussion

This analysis supports the hypothesis that the spring transition in coastal currents is important for successful ocean shrimp recruitment (Hannah, 1993). Although data from this effort and the prior study overlap for 10 of the 16 years presented here, new methods were used in this study that did not depend on constant catchability and were insensitive to failure in the assumption of constant natural mortality and insensitive to assumptions about trawl efficiency. The fact that this study and the earlier effort both found a strong correlation between recruitment and SLH in April of the year of larval release suggests that the interannual variation in shrimp recruitment is substantial, creating a strong "signal" that can be observed through considerable "noise" from various simplifying assumptions.

The precise mechanisms by which a large drop in spring sea levels coincides with strong recruitment of ocean shrimp remains a matter for speculation. This study did not attempt to investigate this issue. A more in-depth discussion of the alternative hypotheses can be found in the earlier paper (Hannah, 1993). The continued importance of April SLH as a strong correlate of shrimp recruitment suggests that further investigation of the potential mechanisms is warranted.

The principal novel finding of this study is the evidence for a stock-recruitment relationship for ocean shrimp. This evidence is statistical in nature and the data series is fairly short, suggesting that this finding should be considered preliminary at this time. The fact that much of the environmental variation in recruitment has been accounted for in the models, in combination with the lack of a serial autocorrelation in the recruitment index, supports the contention that an actual stock-recruitment relationship has been detected (Garcia, 1983). The form of the detected relationship corresponds to the ascending leg of the curve, indicating that some reduction in average recruitment has resulted from low spawner abundance. Unfortunately, the relationship demonstrated gives little indication of the shape of the right hand portion of the curve, leaving the proper functional form an open question.

With environmental variation strongly influencing ocean shrimp recruitment, the detection of a stock-recuitment relationship has different implications from those in a classical application of stock-recruitment theory. In stocks with reasonably stable recruitment, stock-recruitment curve parameters can, in theory, be used to determine a maximum sustainable yield. For shrimp, the multivariate recruitment models (Table 2) define a surface over which recruitment varies in response to the environment and changes in the level of spawning stock. The environmental influence on recruitment also implies a very strong recruitment-stock relationship; the points residing in the lower left corner of Figure 4 are not simply the result of fishing but are due to low recruitment in the parent years, in combination with fishing (Fig. 8). The main value of knowing that a stock-recruitment relationship exists for ocean shrimp is that it suggests strongly that there is a

level of fishing beyond which the average subsequent recruitment will be reduced. The distribution of stock and recruitment data in this study suggests that maintaining a "spawner threshold" for this stock unit should produce higher average recruitment (Fig. 4). The threshold suggested here, 1.3 billion spawning shrimp is, of course, not an absolute measure, but rather a level that is relevant only to the indices as constructed here, assuming elemental trawl efficiency of 0.50. If better information on the average elemental efficiency of shrimp trawl gear can be developed, then an actual spawning threshold can be calculated. With or without an absolute threshold, these data suggest that curtailing harvest in years of recruitment failure has the potential to increase subsequent average recruitment.

One seemingly surprising finding of this study is that egg production seems to offer little benefit over spawner abundance as an index of shrimp reproductive output. This result is partially an artifact caused by the two indices being based on the same underlying estimates of stock area and density, in combination with the use of a static length-fecundity relationship based on pooled data from several samples (Hannah et al., 1995). The egg production index incorporates only two additional sources of real variation: the variation found in the average size of females and in the percentage of females in the spawning population, and these parameters are not highly variable (Hannah et al., 1995). The finding that egg production estimates offer little benefit over estimates of spawner abdundance is also convenient because the flexible sex change exhibited by ocean shrimp makes it difficult to translate an egg production goal into a quantity that can be used to directly manage the fishery, such as a biomass threshold (Charnov et al., 1978; Hannah and Jones, 1991). To do so would require a way to accurately forecast the percentage of both primary females and age-2 males in the fall of the year, a technique not presently available.

The apparent influence of intense fishing on late egg-bearing females in April may have important implications for management of the ocean shrimp stock and suggests an important interaction between recruitment, parent reproductive output, and variation in the ocean environment. If the timing of the spring transition is indeed the critical determinant of ocean shrimp larval survival, then larvae released early and late in the spring may suffer very different fates, depending on when the spring transition occurs. When the transition is late, logic suggests that the magnitude of recruitment may depend very heavily on the survival of late release larvae, the very ones the fishery is capable of impacting heavily by harvesting egg-bearing shrimp. If this hypothesis is correct, it also suggests that environmental variation and the various measures of shrimp reproductive output one might use are confounded. For example, a large larval release in a year with a late transition may be the functional equivalent of a much smaller larval release in a year with an early transition; both result in low numbers of larvae released into favorable ocean conditions. Similarly, the impact on recruitment of harvesting late egg-bearing females could be large or minimal depending on the timing of the transition. For the 1989 year class, the impact was apparently quite severe, owing to a combination of a large catch of egg-bearing shrimp and a moderately high April sea level (Table 1), suggesting a late spring transition. The same amount of harvest may have had minimal impact on recruitment in a year with an early spring transition, when this hypothesis suggests that most of the larvae would have already been released into favorable conditions. Upon close examination, the interaction between variation in the timing of the spring transition and the timing and magnitude of larval release makes it unlikely that any simple measure of reproductive output would have direct explanatory power with regard to the level of subsequent recruitment. Such a mechanism could also be operating to obscure the stock-recruitment relationship in other stocks with an early critical stage and environmentally forced recruitment.

I consider the detection of a stock-recruitment relationship for this species to be a preliminary finding at this time. If this result endures as additional data become available, the implications for management of the ocean shrimp stock are still not entirely clear. Regulations aimed at eliminating, or severely reducing, the harvest of egg-bearing female shrimp in April may help increase average recruitment of ocean shrimp, with very little reduction in short-term yield. If the opening date of the ocean shrimp season were delayed 2–3 weeks, the harvest of egg-bearing shrimp in April would be virtually eliminated in areas 84 and 86 (Fig. 6). In more southern areas, like area 88, a full month delay is needed to eliminate harvest of egg-bearing shrimp (Fig. 6). With 6 months of fishing remaining in the open season, it is unlikely that annual exploitation rates would be greatly affected by a delay in the season opening date. Although major benefits from such a change in management would not accrue in most years, the evidence for a general stock-recruitment relationship suggests that some small increase in long-term average recruitment would result.

The other novel finding of this study concerns the strong recruitment-stock relationship for ocean shrimp, and its implications for managing highly variable, short-lived stocks. The data show that most

(2 of 3 observed) years of low spawner abundance result mainly from recruitment failures at age 1. This finding suggests that the classic management strategies, aimed at maintaining age-1 escapement rates, such as maximum count-per-pound and minimum codend mesh size, are unlikely to be very successful at reducing recruitment variability and increasing average recruitment for ocean shrimp. The reason for this is that by allowing increased escapement from an extremely depressed year class, there will be likely little impact on total spawner abundance. Rather, a strategy that reduces or eliminates exploitation of all age classes, once a year-class failure has been detected, has more potential to increase spawner abundance, simply because the remaining older shrimp may be more abundant than the failed age-1 year class. Another alternative, of course, is to manage at much lower exploitation rates, such that more shrimp survive to spawn at ages 2 and 3, although such a strategy is unlikely to maximize yield. The precise impact on yield of such an approach is difficult to predict without better knowledge of natural mortality rates. Natural mortality rates of ocean shrimp have been shown to vary widely, possibly in response to changes in the abundance of predator stocks (Hannah, 1995), such as Pacific whiting (*Merluccius productus*). Improved estimates of natural mortality rates for shrimp in turn depend on better knowledge of the elemental efficiency of shrimp trawl gear (Hannah, 1995). In addition, changes in management of this fishery should be geared towards maximizing economic rather than biomass yield (PFMC, 1981), suggesting that a comprehensive bioeconomic model is needed before the findings of this study can begin to be used.

Acknowledgment

This paper was funded in part by a grant/cooperative agreement from the National Oceanic and Atmospheric Administration. This project was financed in part with Federal Interjurisdictional Fisheries Act funds (75% federal, 25% state of Oregon funds) through the U.S. National Marine Fisheries Service (contract NA76FI0139). Helpful reviews of early drafts were provided by David Fox and David Sampson.

Literature cited

Abramson, N. J., and P. K. Tomlinson.
1972. An application of yield models to a California ocean shrimp population. Fish. Bull. 70(3):1021–1041.

Chel-ton, D. B., and R. E. Davis.
1982. Monthly mean sea-level variability along the west coast of North America. J. Phys. Oceanog. 12:757–784.

Chelton, D. B., P. A. Bernal, and J. A. McGowan.
1982. Large-scale interannual physical and biological interaction in the California Current. J. Mar. Res. 40(4): 1095–1125.

Charnov, E. L., Gotshall, D. W., and J. G. Robinson.
1978. Sex ratio: adaptive response to population fluctuations in pandalid shrimp. Science (Wash., D.C.) 200: 204–206.

Garcia, S.
1983. The stock-recruitment relationship in shrimps: reality or artefacts and misinterpretations? Oceanogr. Trop 18:25–48.

Geibel, J. J., and R. F. G. Heimann.
1976. Assessment of ocean shrimp management in California resulting from widely fluctuating recruitment. Calif. Fish and Game 62(4):255–273.

Gotshall, D. W.
1972. Population size, mortality rates, and growth rates of northern California ocean shrimp *Pandalus jordani*, 1965 through 1968. Calif. Dep. Fish and Game, Fish Bull. 155:1–47.

Hannah, R. W.
1993. Influence of environmental variation and spawning stock levels on recruitment of ocean shrimp (*Pandalus jordani*). Can. J. Fish. Aquat. Sci. 50:612–622.
1995. Variation in geographic stock area, catchability and natural mortality of ocean shrimp (*Pandalus jordani*): some new evidence for a trophic interaction with Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 52:1018–1029.
1997. Evaluation of methods used to estimate geographic stock area for ocean shrimp (*Pandalus jordani*) from logbook data. Oregon Dep. Fish Wildl., Information Rep. Ser., Fish. 97-6, 17 p.

Hannah, R. W., and S. A. Jones.
1991. Fishery induced changes in the population structure of pink shrimp (*Pandalus jordani*). Fish. Bull. 89:41–51.

Hannah, R. W., S. A. Jones, and M. R. Long.
1995. Fecundity of the ocean shrimp *Pandalus jordani*. Can. J. Fish. Aquat. Sci. 52:2098–2107.

Hannah, R. W., S. A. Jones, and V. H. Krutzikowsky.
1997. Total catch, fishing effort and age and sex composition of the catch, by area for the ocean shrimp (*Pandalus jordani*) trawl fishery, 1980–95. Oregon Dep. Fish and Wildlife, Pink Shrimp Data Series Report, 131 p.

Huyer, A., and R. L. Smith.
1985. The signature of El Niño off Oregon, 1982–83. J. Geophys. Res. 90(C4):7133–7142.

Huyer, A., J. C. Sobey, and R. L. Smith.
1979. The spring transition in currents over the Oregon continental shelf. J. Geophys. Res. 84(C11):6995–7011.

Jones, S. A., R. W. Hannah and J. T. Golden.
1996. A survey of trawl gear employed in the fishery for ocean shrimp *Pandalus jordani*. Oregon Dep. Fish Wildl., Information Rep. Ser., Fish. 96-6, 23 p.

Lo, N.C.H.
1978. California ocean shrimp mesh experiment. Calif. Fish Game 64:280–301.

McConnaughey, R. A., D. A. Armstrong, B. M. Hickey and D. R. Gunderson.
1994. Interannual variability in coastal Washington Dungeness crab (*Cancer magister*) populations: larval advection and the coastal landing strip. Fish. Oceanogr. 3(1)22–38.

Pacific Fishery Management Council.
1981. Discussion draft fishery management plan for the pink shrimp fishery off Washington, Oregon, and California. PFMC, Portland, OR, 169 p.

Rothlisberg, P. C.
1975. Larval ecology of *Pandalus jordani* Rathbun. Ph.D. diss., Oregon State Univ., Corvallis, OR, 117 p.

Rothlisberg, P. C., and C. B. Miller.
1983. Factors affecting the distribution, abundance, and survival of *Pandalus jordani* (Decapoda, Pandalidae) larvae off the Oregon coast. Fish. Bull. 81(3):455–472.

Rothschild, B. J., and M. J. Fogarty.
1989. Spawning-stock biomass: A source of error in recruitment/stock relationships and management advice. J. Cons. Int. Explor. Mer 45:131–135.

Winters, G. H., and J. P Wheeler.
1985. Interaction between stock area, stock abundance, and catchability coeficient. Can. J. Fish. Aquat. Sci. 42:989–998.

Zirges, M. H., M. R. Saelens, and J. E. McCrae.
1982. Total catch and effort tables, and summary biological statistics for pink shrimp caught in Oregon statistical areas 18–28 by month and area 1966–1981; catch numbers expanded by age and sex, effort in hours by vessel type. Inf. Rep. Ser., Fish. No. 82-4. Oregon Dep. Fish Wildl., Newport, OR, 145 p.

Habitat selection and diet of juvenile red porgy, *Pagrus pagrus* (Linnaeus, 1758)

Mary Labropoulou
Department of Biology
University of Crete
P.O. Box 2208, GR-71409 Iraklion, Crete, Greece
Present address: National Center for Marine Research
Agios Kosmas, 166 04 Hellinikon, Greece
E-mail address: mlabro@posidon.ncmr.gr

Athanasios Machias
Institute of Marine Biology of Crete
P.O. Box 2214, GR-71003 Iraklion, Crete, Greece

Nikolaos Tsimenides
Department of Biology
University of Crete
P.O. Box 2208, GR-71409 Iraklion, Crete, Greece

Abstract—The patterns of distribution and feeding habits of juvenile red porgy, *Pagrus pagrus*, were studied for fish collected in experimental trawl surveys carried out along the Cretan continental shelf over a period of four years. Abundance increased significantly in shallow waters, with a maximum between 20 and 50 m for all seasons, negatively correlated to depth and positively correlated to temperature. Patterns of bathymetric distribution were similar for all sizes of juvenile red porgy, varying little among seasons. The fact that no specimens larger than 219 mm FL were caught in the trawlable fishing grounds indicates that larger individuals aggregated over hardbottom areas that could not be sampled by trawling. Feeding intensity varied among the size classes of fish examined. Stomach-content analysis revealed that juvenile red porgy are carnivorous, feeding mainly on decapods. Diet composition did not vary seasonally; decapods were the most important prey throughout the year. However, the composition of the prey consumed varied considerably with predator size, coupled with differences in mean prey sizes found in each size class. Feeding rates of juveniles in terms of both feeding intensity and amount of food consumed were high and increased with fish size. The Cretan continental shelf habitat offers increased growth rate, reduced predation risk, and increased food abundance to juveniles and therefore they direct energy entirely into somatic growth. Juvenile red porgy appeared to be a separate unit, from a management as well as from an ecological point of view. Habitat segregation is of importance; juvenile specimens were differentiated from mature fish on the basis of their selection of bottom type and prey and to a lesser extent by depth.

Manuscript accepted 20 August 1998.
Fish. Bull. 97:495–507 (1999).

Spatial and temporal variation in population attributes, size and age structure, abundance and distribution, generally reflect life history properties of a species. Changes in diet or habitat (or both) during ontogeny are extremely common in fishes (Werner and Gilliam, 1984). Fish partition food resources between species as well as between size classes within a species. Similar mechanisms such as differences in morphological features, foraging behavior, period of activity and habitat use, affect segregation of resource use in both cases (Werner, 1979; Mittelbach, 1981; Ross, 1986; Norton, 1991). However, different ecological processes have been emphasized in interpreting the adaptive value of resource partitioning in these two situations. Partitioning among species has been argued to reduce interspecific competition (Sale, 1979; Osenberg et al., 1992; Schluter, 1994). By contrast, differential vulnerability to predators or the ability to exploit prey (or both) may lead to *de facto* partitioning of prey among age classes within a species, with the consequence that intraspecific competition is reduced (Werner et al., 1983). Many fish undergo ontogenetic changes in prey use between young-of-year and older stages. Both the ability to utilize the full spectrum of prey and to escape predators may be highly size related. Apart from changes in foraging demands, the vulnerability to predators decreases with increasing body size. Smaller fish frequently use sheltered habitats to reduce predation risk, whereas larger fish are often found in unprotected areas (Miller, 1979; Werner and Hall, 1988; McCormick, 1989). As a result of these changes in life style, fish may occupy different niches during ontogeny (Liem, 1984; Werner and Gilliam, 1984).

The red porgy, *Pagrus pagrus* (Linnaeus 1758), is a protogynous, sublittoral, demersal marine fish associated with a variety of temperate to subtropical habitats in the Atlantic and the Mediterranean Sea. It is commonly found on sandy, gravel, and hard bottoms, or around rocks, at depths ranging from 18 to 185 m (Manooch and Hassler, 1978; Vaughan et al., 1992). The correlation of age with maturity suggests that the majority of the females reach sexual maturity at three years (Manooch, 1976; Pajuelo and

Lorenzo, 1996; Harris and McGovern, 1997). The red porgy is of great commercial importance and consequently a highly exploited species in the areas of its distribution (Manooch and Hassler, 1978; Stergiou and Pollard, 1994). It is one of the most promising new species for fish farming in the Mediterranean Sea, having remarkably high growth rates under intensive rearing conditions. Therefore, the ambient demands of young individuals are of special interest for aquaculture (Divanach et al., 1993). The young individuals are distributed inshore of the adult population in trawlable areas. Even though they occur inshore as juveniles, adverse conditions of low water temperatures, competitive exclusion and unsuitable substrate reduce the longevity of this inshore distribution. Adult red porgy do not occur in the same shallow waters as those inhabited by juveniles. The larger fish predominate in deeper waters, preferring hard substrate (Manooch and Hassler, 1978). A general trend for larger fish to occur in deeper water has long been known with respect to deep sea fishes (Haedrich and Rowe, 1977); however it has also been mentioned by Macpherson and Duarte (1991) for many demersal fishes of the continental shelf. Caddy (1993) has stated that offshore movements of older fish to locations on untrawlable bottoms possibly contribute to the continuing good recruitment, as well as to the stock recovery.

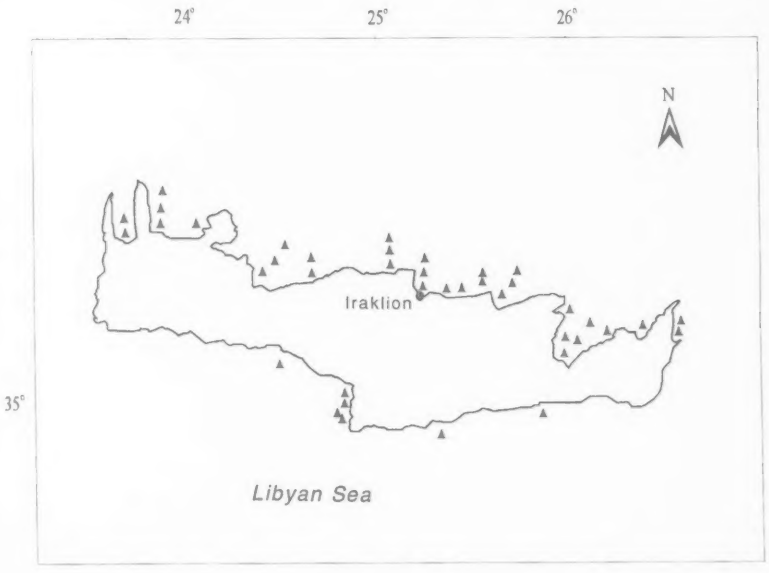


Figure 1
Location of the sampling stations on the Cretan continental shelf.

The aim of the present study was to define the habitat use of juvenile red porgy along the Cretan continental shelf and to examine whether red porgy undergo considerable changes in resource utilization during ontogeny. In addition to determining bathymetric trends in mean size of red porgy, the relationship between density, depth, and temperature within size groups are defined. Furthermore, we investigated the effects of the feeding habits, prey choice, and trophic interactions among the different size groups on the distribution patterns of red porgy.

Material and methods

Study area and sampling procedure

A three-year survey on the distribution of red porgy was carried out along the Cretan continental shelf, from August 1988 to April 1991. Nine seasonal experimental bottom trawl survey cruises were conducted by the Institute of Marine Biology of Crete at 40 fixed sampling stations selected to cover all the trawlable fishing grounds of the region (Fig. 1). The collected data included abundance of fishes caught and supporting data on depth, temperature, and salinity. The cruise periods were as follows: late August to early September (summer), December (winter), and late March to early April (spring). The sampling stations were distributed over three distinct depth zones: 26–70 m (zone I), 71–150 m (zone II), and 151–350 m (zone III). Zone I covered 25%, zone II 24%, and zone III 51% of the total study area. Algae and marine angiosperms, mainly *Caulerpa prolifera*, *Posidonia oceanica*, and *Halophila stipulacea*, dominated the sand-silt substrate in zone I. The substrate of zone II was muddy and the substrate of zone III was covered by the crinoid *Leptometra phalangium*. Monthly samples (excepting January) from August 1990 to August 1992 were also taken from experimental trawl surveys in Iraklion Bay for stomach-content analysis. These samples were collected from a fixed station on the trawlable fishing ground of the region between 25 and 35 m during the morning, between 0830 and 0930 hours.

The trawl used was equipped with a codend bag liner of 22-mm stretched mesh size. The duration of each haul (bottom time) was 50–90 min and the trawling speed fluctuated from 1.8 to 3 knots, depending on the depth and nature of the bottom. Be-

cause all trawls were carried out with the RV *Philia*, it was assumed that gear selectivity was constant. Bottom temperature and salinity were measured with a SEA-BIRD CTD unit. The measurements recorded for the 5 m above the bottom of each station were averaged and the resulting values were considered as the temperature and salinity at the specific station.

Laboratory methods

Fork lengths (FL, mm) were measured for at least 100 individuals collected at each station and cruise. Of a total of 3280 fish, all specimens were found to be immature. To evaluate size-related variations in food habits and habitat use, red porgy were separated into five size classes: 0 (40–104 mm FL), 1 (105–147 mm FL), 2 (148–186 mm FL), 3 (187–219 mm FL), and 4 (>219 mm FL) which were chosen as they approximate the age of the fish within each size class as determined from the von Bertalanffy growth equation derived by Machias et al. (1998).

Each month 20–30 specimens were preserved in 10% buffered formalin immediately after capture for stomach-content analysis. Samples were taken to the laboratory, measured to the nearest mm (FL), and weighed to the nearest 0.1 g. Thereafter, the stomachs were removed and the contents wet weighed. Prey items were identified to the lowest possible taxonomic level, counted under a binocular microscope and weighed to the nearest 0.01 g. Prey species were measured to the nearest 0.1 mm by using an ocular micrometer or a vernier caliper, where possible. Fork length of the fish examined ranged from 41 to 185 mm, mean (±SD) FL was 87.2 (±26.9) mm.

Data analysis

In accordance with the procedure described by Carrothers (1980), the door spread of the trawl net was calculated for each haul and then multiplied by the speed of the boat and fishing time to estimate the total area sampled. The abundance of fish caught was expressed as number of individuals per square nautical mile (nmi^2), making the comparison of fish abundance between sampling stations possible. After logarithmic transformations (Middleton and Musick, 1986; Stefanescu et al., 1992), mean abundances (number/nmi^2) were calculated for each cruise: 1) for 20-m depth intervals, 2) for 50-m depth intervals, and 3) per zone (I, II, III), as well as for each 1°C temperature interval. Salinity showed little variation (Table 1), having no effect on the distribution of fishes on the Cretan shelf (Tsimenides et al., 1991).

Analysis of variance showed no significant differences in the mean abundance among the three surveys in each season, nor among each zone during the same season ($0.377<P<0.610$, Bartlet test $0.201<P<0.462$). Results and conclusions for each season were similar and independent of whether survey-specific or pool data were used. Hence, only the latter are presented. Correlation analyses (Pearson correlation coefficient) were performed to determine if there were any significant changes in abundance with depth and water temperature, as well as to test the hypothesis that fish size was depth or temperature dependent. Geometric mean was preferred for calculating the mean fish size of each sample, because the arithmetic mean is susceptible to the influence of few large specimens and does not accurately represent the central tendency in fish size at a given station (Stefanescu et al., 1992). The bathymetric distribution of different size fish was simplified by converting lengths into the above-mentioned five size classes.

The contribution of prey items to diet was estimated by using both the numerical abundance and the biomass of prey items in stomachs (Berg, 1979; Hyslop, 1980; Bowen, 1983). Breadth of diet was calculated by using Levin's standardized index (Hurlbert, 1978; Krebs, 1989):

$$B_i = \frac{1}{n-1}\left(\frac{1}{\sum_j p_{ij}^2} - 1\right),$$

where B_i = Levin's standardized index for predator i;
p_{ij} = proportion of diet of predator i that is made up of prey j; and
n = number of prey categories.

This index ranges from 0 to 1; low values indicated diets dominated by few prey items (specialist predators), higher values indicated generalist diets (Gibson and Ezzi, 1987; Krebs, 1989). Diet overlap between the size classes was calculated by using the simplified Morisita's index (Krebs, 1989; Hall et al., 1990):

$$C_{ik} = \frac{2\sum_j p_{ij} p_{kj}}{\sum_j p_{ij}^2 + \sum_j p_{kj}^2},$$

where C_{ik} = simplified Morisita's index for predators i and k; and
p_{ij} and p_{kj} = proportions of predator i and k with prey j in their stomachs.

Diet overlap increases as the Morisita's index increases from 0 to 1. Overlap is generally considered

to be biologically significant when the value exceeds 0.60 (Keast, 1978; MacPherson, 1981; Wallace, 1981; Langton, 1982). Bias-corrected bootstrap 95% confidence intervals, based on 1000 simulations, were used to estimate the reliability of these indices (Efron and Tibshirani, 1986; Hall et al., 1990). Differences in diet composition and stomach fullness by fish size and month were tested by χ^2 on combined data for both years because diet did not vary significantly between the two years. The logit model used to investigate monthly variations in the proportion of full and empty stomachs, as a function of fish size was

$$\log (p_d/p_d - 1) = a_d + b_d L + e$$

where p_d = the probability that a stomach is nonempty in month d;
L = the fish length; and
e = the error term.

One-way ANOVAs were used to compare the mean number, the mean weight, and the mean size of prey items among the size classes and the *a posteriori* Tukey's test was employed to locate the source of any differences. Numbers and weights of prey items were log-transformed to remove the dependency of the variance on the mean (Zar, 1984). Mean number and mean weight of prey per fish in each size class was based only on specimens with food items in their stomach. All statistical inferences were based on the 0.05 significance level.

Results

Distribution patterns

Red porgy were found to occur to 250 m depth, between temperatures of 14.5 and 24.2°C and salinities of 38.1 and 40.0‰ (Table 1). Abundance in the trawlable fishing grounds was negatively related to depth during all seasons and positively related to temperature during summer and winter (Table 2). No significant correlations between abundance and temperature were observed during spring.

The distribution of red porgy by depth intervals indicated that although fish generally occur in all zones, their abundance significantly increased in shallow waters (zone I), with highest values during summer (Fig. 2). Relative abundance was significantly higher in the shallow zone, with a maximum between 20 and 50 m depth for all seasons. Furthermore, the relative abundance increased progressively from winter to a maximum of 2985.6 individuals per nmi^2 in summer. These differences of the relative abundance in the shallow zone were mainly due to recruitment during summer.

Table 1

Seasonal ranges of depth and temperature over the Cretan shelf where *Pagrus pagrus* occurred.

	Minimum	Maximum	Range
Depth (m)			
Spring	30	110	80
Summer	28	210	182
Winter	29	250	221
Temperature (°C)			
Spring	14.5	17.3	2.8
Summer	14.5	24.2	9.7
Winter	15.0	17.8	2.8
Salinity (S‰)			
Spring	38.66	39.05	0.39
Summer	38.12	39.72	1.60
Winter	38.65	39.99	1.34

The relationships between mean FL and depth were significantly positive in summer and winter (Table 2). Maximum FL increases with depth only in summer, whereas the minimum and the mean FL increase during summer and winter. However, no significant correlation between FL and temperature was found (Table 2). Depth distribution by size revealed that fish larger than 186 mm do not occur in shallow waters, which were dominated by young fish (Fig. 3). Moreover, individuals larger than 147 mm were poorly represented at depths below 80 m. The abundance of the size classes 0–2 was greatest in warm waters during all seasons (Fig. 4).

Feeding intensity

Of the 634 stomachs of red porgy examined, 226 were found to be empty (35.7%). The proportion of empty stomachs varied significantly among the size classes of fish examined (χ^2=11.78, P<0.001), with a maximum of 39.6% for the 0 size class (Table 3). The logit model revealed that the interaction between month and fish size on the probability that a stomach is nonempty was significant (F=2.07, P<0.01). The slope was always >0, indicating a positive allometry on full stomachs, whereas no differences on the estimated probabilities were detected between the two years (t-test=–0.50, P>0.05).

Composition of the diet

There were at least 58 different prey species belonging to four major groups (decapods, small crusta-

Table 2

Correlation analysis between *Pagrus pagrus* abundance and fork length with depth and temperature. *r*: Pearson correlation coefficient, *P*: significant level of probability.

	Abundance		Mean fork length (mm)		Minimum fork length (mm)		Maximum fork length (mm)	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Depth (m)								
Spring	–0.524	0.03	0.084	0.79	0.207	0.52	0.217	0.50
Summer	–0.621	0.00	0.693	0.00	0.670	0.00	0.689	0.00
Winter	–0.598	0.00	0.701	0.00	0.685	0.01	0.167	0.58
Temperature (°C)								
Spring	0.224	0.10	0.633	0.07	0.070	0.85	0.585	0.10
Summer	0.787	0.00	0.401	0.25	0.510	0.13	0.621	0.06
Winter	0.349	0.01	0.138	0.74	0.097	0.82	0.299	0.47

Table 3

Feeding indices of *Pagrus pagrus* from the Cretan shelf, in relation to size.

Size class	Fork length (mm)	No. of stomachs analysed	No. of full stomachs	Mean no. of prey items per stomach[1]	Mean weight prey items (g) per stomach[1]	No. of prey species	Diet breadth (Levin's index)[2]	
							Number	Biomass
0	42–104	450	271	2.96[a] (± 0.23)	0.17[a] (± 0.01)	45	0.39 (0.22–0.50)	0.45 (0.31–0.56)
1	105–145	161	117	1.98[b] (± 0.20)	0.46[b] (± 0.01)	36	0.38 (0.22–0.50)	0.29 (0.15–0.38
2	146–185	23	20	2.23[b] (± 0.30)	0.77[c] (± 0.01)	27	0.373 (0.21–0.49)	0.20 (0.12–0.33)

[1] Standard error given in parentheses, different letters indicate significant differences among means (Tukey's test).
[2] Ranges in parentheses: 95% bootstrap confidence intervals.

ceans, polychaetes, and fish) (Table 4). Polychaetes predominated in terms of percentage by number (35.1%), whereas decapods made up 54.2% of the total weight of stomach contents. Small crustaceans were also consumed in fairly large proportions by number (25.2%), but their contribution by weight was minor. Fish were a considerable dietary staple by weight (23.5%), although their contribution by number (6.7%) was comparatively low. At the species level, the thalassinid *Upogebia tipica*, the caprellid *Phtisica marina,* and the sedentary polychaete *Terebellides stroemi* were the most exploited prey. Among fish prey, *Gobius niger* was the species having greatest contribution in the diet of red porgy. Diet breadth was found to be 0.39 (±0.01) for the numerical abundance and 0.31 (±0.07) for the biomass of the prey species.

Food in relation to fish size

Although the contribution of prey groups, in terms of both number and weight, varied with fish size (Table 4), there were significant differences only between ingestion of small crustaceans (χ^2=28.46, P<0.001), *U. tipica* (χ^2=15.38, P<0.001), and *Liocarcinus maculatus* (χ^2=8.24, P<0.01). Small crustaceans occurred in the younger specimens (0 size class), whereas *U. tipica* and *L. maculatus* occurred in greater percentages in the diet of fish corresponding to size classes 1 and 2. The total amount of food ingested varied significantly among size classes (F=51.95, P<0.001). Pair-wise group comparisons showed three homogeneous groups: the mean consumption rate per individual (i.e. g food/size class)

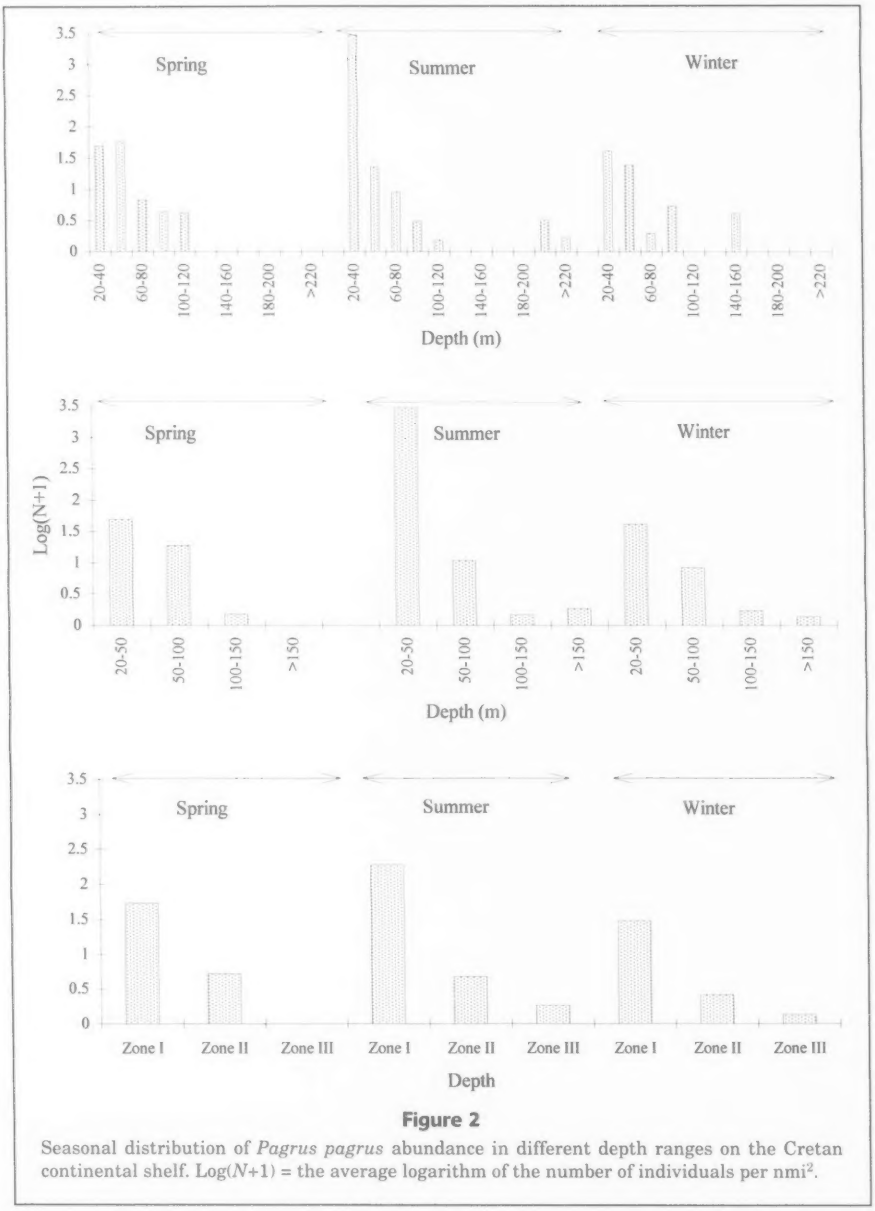


Figure 2

Seasonal distribution of *Pagrus pagrus* abundance in different depth ranges on the Cretan continental shelf. Log(N+1) = the average logarithm of the number of individuals per nmi^2.

increased with increasing size, with 0-size-class fish to exhibit the lowest consumption rate (Table 3). The mean number of prey items consumed decreased significantly with size (F=3.33, P<0.05) (Table 3).

Breadth of diet decreased with fish size, both numerically (abundance) and with biomass of prey species (Table 3). In general, values for dietary overlap between size classes were similar irrespective of the resource matrix used. A significantly high overlap was observed only between specimens of 1 and 2 size classes (Table 5).

Seasonal variation in diet

Diet composition was fairly consistent over the months (Fig. 5, A and B). Decapods were the most important prey throughout the year, especially during winter months and March, owing to the increase of the importance of the thalassinid *U. tipica*. Polychaetes were also an important component in the diet of red porgy throughout the year. Dietary breadth varied little, except for low values in winter months

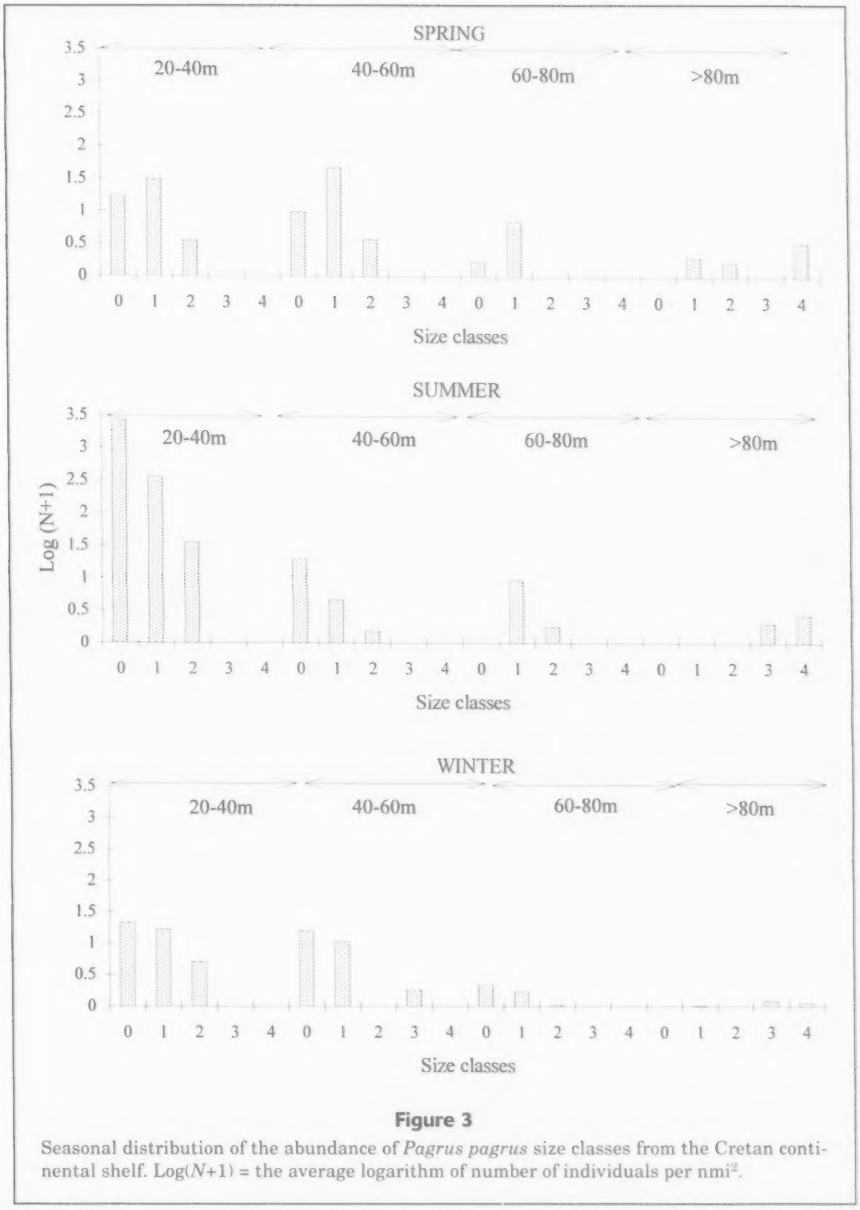


Figure 3

Seasonal distribution of the abundance of *Pagrus pagrus* size classes from the Cretan continental shelf. Log(N+1) = the average logarithm of number of individuals per nmi^2.

and March, when *U. tipica* dominated (Fig. 6, A and B).

Relationship of length of predator to length of prey

Significant positive correlations were found between the size of red porgy and the mean size of prey consumed (P<0.001, r^2=0.85, n=169). Furthermore, analysis of variance on the mean prey sizes consumed by the three size classes revealed significant differences (F=93.7, P<0.001). The 0-year fish exploited prey with smallest mean size (18 ±6.6 mm), 1-year fish consumed prey 26.2 ±5.4 mm, and 2-year fish fed on the largest prey (41.6 ±5.8 mm).

Discussion

Juvenile red porgy on the Cretan continental shelf tend to occur in shallows (20–50 m), where the sub-

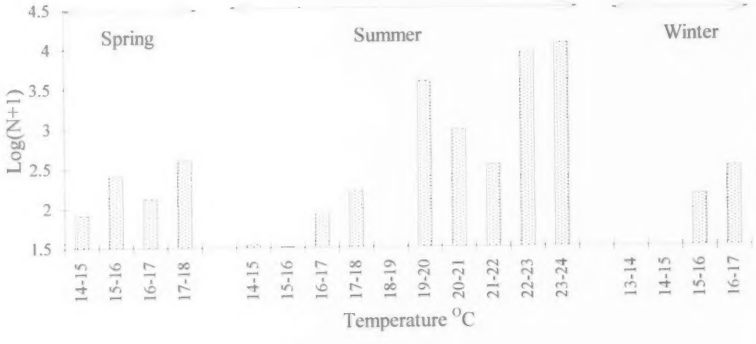


Figure 4

Seasonal distribution of *Pagrus pagrus* abudance in 1°C temperature intervals, on the Cretan continental shelf. Log(N+1) = the average logarithm of number of individuals per nmi^2.

strate is sandy and interspersed with patches of algae and seagrass. At this depth range, bottom water temperature is the highest during all seasons. Thus, this depth preference is consistent with the tendency for red porgy to select warm temperatures in relation to those available in other areas of its distribution (Manooch and Huntsman, 1977; Manooch and Hassler, 1978; Pajuelo and Lorenzo, 1996). Although red porgy were found to occur down to 250 m depth, their densities were significantly greater at shallow stations. Furthermore, specimens smaller than 186 mm predominated in the trawl catches, whereas relative abundances of larger specimens was low. High densities of red porgy in shallow waters were due to the large number of juveniles, i.e. specimens that have not reached sexual maturity (Manooch and Hassler, 1978). The lack of larger fish from the trawl catches in shallower depths could not be due to gear selectivity because larger specimens were occasionally found in deeper waters, indicating that they could have also been caught in shallower depths, if present. A similar distribution pattern has also been reported for the Indo-Pacific species *Pagrus auratus* which has been studied in many different areas (Azeta et al., 1980; Kingett and Choat, 1981; Tanaka, 1985).

Size (or age) tends to be positively correlated with depth in many demersal fishes. Tremblay and Sinclair (1985) reported that the mean depth of occurrence tended to increase with age of cod in the southern Gulf of St. Lawrence. Similarly, Sinclair (1992) noted a positive correlation between age and median depth of cod on the eastern Scotian Shelf. Macpherson and Duarte (1991) found that mean fish length increased with depth in most south-east Atlantic and north-west Mediterranean demersal fishes. Bathymetric trends in demersal fish distribution may be linked to other physical factors correlated with depth (e.g. temperature, salinity, bottom type). Temperature is a key factor in the metabolism of fishes and many studies have reported relationships between temperature and fish distribution (Fry, 1971; Nakken and Raknes, 1987; Rose and Leggett, 1989; Macpherson and Duarte, 1991). However it is unlikely that fish distributions are determined by physical factors alone. Biotic factors, in particular prey abundance, have also been shown to be important determinants of distribution. Productivity generally decreases with increasing depth and distance from land; therefore prey resources are greater in shallow waters. Haedrich and Rowe (1977) concluded that selection for mobility and metabolic efficiency should favor larger size in the relative barren deep sea, whereas Macpherson and Duarte (1991) suggested that the positive size-depth relationship in demersal fish may result from age-specific differences in temperature preferences. They argued that younger fish occupy warmer waters, where food supply and growth rates may be greater, whereas older fish occupy colder waters, where they may benefit from lower metabolic costs and greater longevity.

The most striking aspect of our results, was the lack of variation in the bathymetric pattern of red porgy and the fact that depth distribution varied little among size classes, during all seasons. The scarcity of specimens larger than 187 mm in the bathymetric range >50 m is noteworthy, especially for a species with a life span more than 12 years (Vassilopoulou and Papaconstantinou, 1992). Thus the absence of mature specimens in trawl nets during the present

Table 4

Percentage contribution by number (*n*) and by weight (*w*) of the major prey taxa and species in the diet of each size class of *Pagrus pagrus* from the Cretan shelf. Prey occurring in >1% of the total are given. (+ = <1%; – indicates absence).

	n			*w*		
	Size classes			Size classes		
Prey category	0	1	2	0	1	2
Mysids	1.76	+	–	+	+	–
Polychaetes						
Terebellides stroemi	12.13	14.62	2.63	9.11	6.43	+
Aponuphis bilineata	7.35	9.67	–	5.22	2.57	–
Onuphidae	9.82	+	–	7.31	+	–
Glycera rouxii	+	11.12	4.13	+	4.22	1.03
Laetmonice hystrix	+	+	4.78	+	+	1.11
Other species	5.33	3.74	5.71	2.90	3.29	+
(Total polychaetes)	34.64	39.15	17.24	24.54	16.52	2.91
Small crustaceans						
Phtisica marina	20.95	+	–	+	+	–
Leptochelia savignyi	7.95	+	–	+	+	–
Apherusa chiereghinii	2.78	+	–	+	+	–
Other species	1.07	–	–	+	–	–
(Total small crustaceans)	32.75	+	–	+	+	–
Decapods						
Processa nouveli	2.14	+	–	2.47	+	–
Upogebia tipica	11.71	23.58	37.93	38.12	27.63	38.69
Paguridae	4.16	9.91	3.45	6.66	10.60	4.82
Ethusa mascarone	+	3.30	6.90	+	3.83	+
Liocarcinus sp.	+	2.83	–	+	4.00	–
Liocarcinus maculatus	1.76	6.13	24.14	2.49	5.74	26.13
Other species	2.14	+	–	3.11	+	–
(Total decapods)	21.91	46.69	72.42	52.85	52.20	70.15
Fish						
Gobius sp.	+	1.89	–	1.88	11.00	–
Gobius niger	+	4.25	6.90	5.34	9.22	23.52
Mullus barbatus	–	–	3.45	–	–	3.42
Other species	5.04	1.88	–	12.95	6.28	–
(Total fish)	5.79	8.02	10.35	19.47	26.50	26.94
Others	3.15	5.19	–	2.58	4.78	–

study almost certainly reflects aggregations of larger individuals on hard bottoms that were not trawlable. The maximum abundance of juveniles at 20–50 m could be related to the major availability of food resources at this depth range. Because nearshore areas typically contain a greater abundance of food (e.g. Hawkins et al. 1985; Swain, 1993) and a lower incidence of teleost predators (Werner and Gilliam, 1984; L' Abée-Lund et al., 1993; Ruiz et al., 1993), aggregations of young red porgy into shallow zone will result in an increase rate of growth and a lower mortality of these juveniles.

The composition of food suggests that the red porgy is a carnivorous species that relies on epibenthic invertebrates, mainly decapods. Despite the large number of taxa found in stomach contents, few species accounted for most of the prey consumed. The fact that the mean number of prey items per stomach was small (there was also a tendency for number of prey to decrease with fish size), indicates an active selection for prey taxa of large size. Moreover, specimens of each size class showed a further trend towards segregation of their feeding niches by consuming dif-

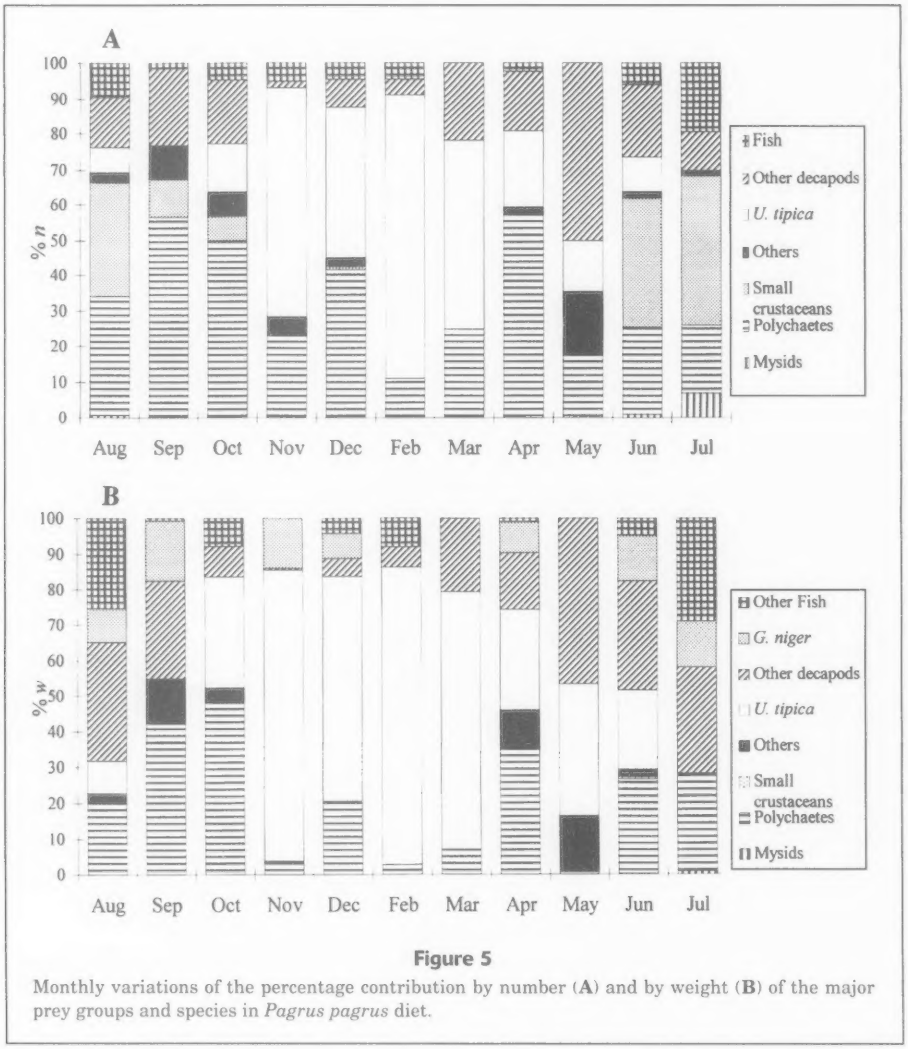


Figure 5

Monthly variations of the percentage contribution by number (**A**) and by weight (**B**) of the major prey groups and species in *Pagrus pagrus* diet.

ferent prey sizes. There is evidence that prey size differences reflect changing food preference with fish size, as well as the ability of larger individuals to capture larger animals. Mean prey-size increases with increasing predator size so that the energy return per unit of effort is optimal. The relatively high percentage of empty stomachs found in the 0 size class and the positive allometry on full stomachs suggest that feeding intensity increased with fish size. These results are not consistent with the general tendency of a decreased rate of metabolism typical of larger fish found in many studies (e.g. Smith and Page, 1969; Martin, 1970; Kislialioglu and Gibson, 1976; Fange and Grove, 1979; Werner, 1979; Grove and Crawford, 1980; Robb and Hislop, 1980), presumably because the specimens examined were immature. Hence it may be concluded that feeding rates exhibited by juveniles were high in terms of both feeding intensity and the amount of food consumed. Because red porgy on the Cretan shelf does not become mature until the third year of life, it remains for a long period in highly productive shallow waters and thus directs its effort entirely into somatic growth. The resultant increase in body size would thereby lead to an increase in the fecundity of individuals when they do, finally, become mature (Stearns, 1992).

Papaconstantinou and Caragitsou (1989) reported that in specimens >200 mm FL the importance of decapods, fish, and polychaetes declined rapidly with size, being replaced by anthozoans, brachyurans, and echinoderms. Unlike the results of the present study,

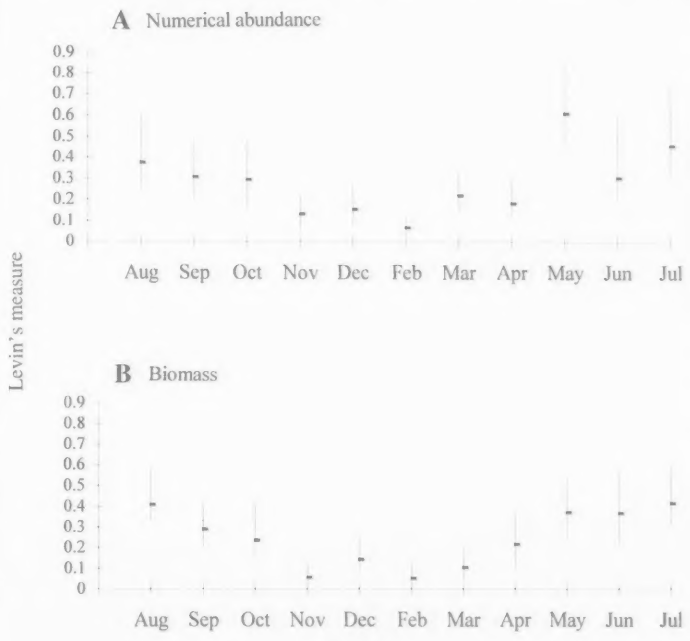


Figure 6

Monthly variations of *Pagrus pagrus* dietary breadth: numerical abundance (**A**); biomass (**B**). Error bars are 95% bootstrap confidence intervals.

their results showed pronounced seasonal changes in the diet of red porgy. It is possible that these differences in feeding habits between juvenile and mature individuals are associated with habitat change from soft bottom to hard substrates. Manooch (1977) stated that red porgy is an opportunistic browser feeding on a variety of invertebrates as well as small fish. He also noted that its diet appeared to be dependent on species availability, rather than preference or selection. These differences between our results and those of the previous studies may be due in part to the fact that in both studies dietary analysis was based on mature specimens, probably reflecting the distinct spatial zones occupied by juvenile and mature specimens.

According to our results, habitat of juvenile red porgy appears to be well separated from that of adult specimens. The absence of mature individuals in the trawlable fishing grounds indicates that recruitment in shallow waters is followed by an ontogenetic movement to a new habitat, at the time they reach sexual maturity. Further examination of this phenomenon is important from a biological, as well as from a management, point of view. Red porgy have previously been described as a food generalist obtaining most of its food from the benthos and epibenthos as well as a habitat generalist occupying a variety of habitats (Manooch, 1977; Manooch and Hassler, 1978; Pajuelo and Lorenzo, 1996). Patterns observed in the

Table 5

Diet overlap for the three size classes (0, 1, and 2) of *Pagrus pagrus* based on the numerical abundance and biomass of prey species. Ranges in parentheses: 95% bootstrap confidence intervals. Significantly high overlap values are in bold.

	Biomass	
Size class	0	1
1	0.44 (0.32–0.56)	
2	0.31 (0.18–0.48)	**0.73 (0.67–0.82)**
	Numerical abundance	
Size class	0	1
1	0.51 (0.31–0.66)	
2	0.36 (0.19–0.47)	**0.72 (0.57–0.84)**

present study suggest that habitat segregation is of importance; juvenile specimens are differentiated from mature ones on the basis of the bottom type and prey selection and to a lesser extent on the basis of depth.

Literature cited

Azeta, M., R. Ikemoto, and M. Azuma.
1980. Diurnal activity rhythms in 0-group red sea bream, *Pagrus major*. Bull. Seikai. Reg. Fish. Res. Lab. 54:279–289.

Berg, J.
1979. Discussion of methods of investigation the food of fishes with reference to a preliminary study of the prey of *Gobiusculus flavencens*. Mar. Biol. 50:263–273.

Bowen, S. H.
1983. Quantitative description of the diet. *In* L. A. Nielsen and D. L. Johnson (eds), Fisheries techniques p. 325–336. Am. Fish. Soc., Bethesda, MD.

Caddy, J. F.
1993. Some future perspectives for assessment and management of Mediterranean fisheries. Sci. Mar. 57:121–130.

Carrothers, P. J. G.
1980. Estimation of trawl door spread from wing spread. J. Northwest Atl. Fish. Sci. 1:81–89

Divanach, P., M. Kentouri, G. Charalambakis, F. Pouget, and A. Sterioti.
1993. Comparison of growth performance of six Mediterranean fish species reared under intensive farming conditions in Crete (Greece), in raceways with the use of self feeders. *In* G. Barnabé and P. Kestemont (eds.), Production, environment and quality, p. 285–297. Special Publication 18, Ghent, Belgium.

Efron, B., and R. Tibshirani.
1986. Bootstrap methods for standard errors, confidence intervals and other measures of statistical accuracy. Stat. Sci. 1:54–77.

Fange, R., and D. Grove.
1979. Digestion. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (eds), Fish physiology, p. 161–260. Academic Press, New York, NY.

Fry, F. E. J.
1971. The effect of environmental factors on the physiology of fish. *In* W. S. Hoar, D. J. Randall and J. R. Brett (eds.), Fish physiology, vol. VI, p. 1–98. Academic Press, New York, NY.

Gibson, R. N., and I. A. Ezzi.
1987. Feeding relationships of a demersal fish assemblage on the west coast of Scotland. J. Fish Biol. 31:55–69.

Grove, D., and C. Crawford.
1980. Correlation between digestion rate and feeding frequency in the stomachless teleost *Blennius pholis* L. J. Fish Biol. 16:235–247.

Haedrich, R. L., and G. T. Rowe.
1977. Megafaunal biomass in the deep sea. Nature 269: 141–142.

Hall, S. J., D. Raffaelli, D. J. Basford, M. R. Robertson, and R. Fryer.
1990. The feeding relationships of the larger fish species in a Scottish sea loch. J. Fish Biol. 37: 775–791.

Harris, P. J., and J. C. McCovern.
1997. Changes in the life history of the red porgy, *Pagrus pagrus*, from the southeastern United States, 1972–1994. Fish. Bull. 95:732–747.

Hawkins, A. D., N. M. Soofiani, and G. W. Smith.
1985. Growth and feeding of juvenile cod (*Gadus morhua* L.). J. Cons. Int. Explor. Mer 42:11–32.

Hurlbert, S. H.
1978. The measurement of niche overlap and some relatives. Ecology 59: 67–77.

Hyslop, E. J.
1980. Stomach contents analysis-a review of methods and their application. J. Fish Biol. 17:411–429.

Keast, A.
1978. Trophic and spatial interrelationships in the fish species of an Ontario temperature lake. Env. Biol. Fish. 3:7–31.

Kingett, P. D., and J. H. Choat.
1981. Analysis of density and distribution patterns in *Chrysophrys auratus* (Pisces: Sparidae) within a reef environment: an experimental approach. Mar. Ecol. Prog. Ser. 5:283–290.

Kislialioglu, M. and R. N. Gibson.
1976. Prey "handling time" and its importance in food selection by the 15-spined stickleback, *Spinachia spinachia* (L.). J. Exp. Mar. Biol. Ecol. 25:151–158.

Krebs, C. J.
1989. Ecological methodology. Harper and Row, New York, NY, 654 p.

Langton, R. W.
1982. Diet overlap between Atlantic Cod, *Gadus morhua*, Silver Hake, *Merluccius bilinearis* and fifteen other Northwest Atlantic finfish. Fish. Bull. 80:745–759.

Liem, K. F.
1984. Functional versality, speciation, and niche overlap: are fishes different? *In* D. G. Meyers and J. R. Strickler (eds), Trophic interactions within aquatic ecosystems, p. 269–305. Westview Press, Boulder.

L' Abée-Lund, J. H., A. Langeland, B. Jonsson, and O. Ugedal.
1993. Spatial segregation by age and size in Arctic charr: a trade-off between feeding possibility and risk of predation. J. Anim. Ecol. 62:160–168.

Machias, A., N. Tsimenides, L. Kokokiris, and P. Divanach.
1998. Ring formation on otoliths and scales of *Pagrus pagrus*: a comparative study. J. Fish Biol. 52: 350-361.

MacPherson, E.
1981. Resource partitioning in a Mediterranean demersal fish community. Mar. Ecol. Prog. Ser. 4:183–193.

MacPherson E., and C. M. Duarte.
1991. Bathymetric trends in demersal fish size: is there a general relationship? Mar. Ecol. Prog. Ser. 71:103–112.

Manooch, C. S.
1976. Reproductive cycle, fecundity and sex ratios of the red porgy, *Pagrus pagrus* (Pisces: Sparidae) in North Carolina. Fish. Bull. 74:775–781.
1977. Foods of the red porgy, *Pagrus pagrus* Linnaeus (Pisces: Sparidae), from North Carolina and South Carolina. Bull. Mar. Sci. 27:776–787.

Manooch, C. S., and W. W. Hassler.
1978. Synopsis of biological data on the red porgy, *Pagrus pagrus* (Linnaeus). U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 412:1–19.

Manooch, C. S., and G. R. Huntsman.
1977. Age, growth and mortality of the red porgy, *Pagrus pagrus*. Trans. Am. Fish. Soc. 106:26–33.

Martin, N. V.
1970. Long-term effects of diet on the biology of the lake

trout and the fishery in Lake Opeongo, Ontario. J. Fish. Res. Board Can. 27:125–146.

McCormick, M. I.
1989. Spatio-temporal patterns in the abundance and population structure of a large temperate reef fish. Mar. Ecol. Prog. Ser. 53:215–225.

Middleton R. W., and J. A. Musick.
1986. The abundance and distribution of the family Macrouridae (Pisces: Gadiformes) in the Norfork Canyon area. Fish. Bull. 84:35–62.

Miller, R. J.
1979. Relationships between habitat and feeding mechanisms in fishes. *In* R. Stroud and H. Clepper (eds), Predator-prey systems in fisheries management, p. 269–280. Sport Fishing Inst. Wash., D.C.

Mittelbach, G. G.
1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62:1370–1386.

Nakken, O., and A. Raknes.
1987. The distribution and growth of Northeast Arctic cod in relation to bottom temperatures in the Barents Sea, 1978–1984. Fish. Res. 5:243–252.

Norton, S. F.
1991. Habitat use and community structure in an assemblage of cottid fishes. Ecology 72:2181–2192.

Osenberg, G. W., G. G. Mittelbach, and P. C. Wainwright.
1992. Two-stage life histories in fish: the interaction between juvenile competition and adult performance. Ecology 73:255–267.

Pajuelo, J. G., and J. M. Lorenzo.
1996. Life history of the red porgy *Pagrus pagrus* (Teleostei: Sparidae) off the Canary islands, central east Atlantic. Fish. Res. 28:163–177.

Papaconstantinou, C., and E. Caragitsou.
1989. Feeding interaction between two sympatric species *Pagrus pagrus* and *Phycis phycis* around Kastellorizo Island (Dodecanese, Greece). Fish. Res. 7:329–342.

Robb, A. P., and J. R. G. Hislop.
1980. The food of five gadoid species during the pelagic 0-group phase in the northern North Sea. J. Fish Biol. 16:199–217.

Rose, G. A., and W. C. Leggett.
1989. Interactive effects of geophysically-forced sea temperatures and prey abundance on mesoscale coastal distributions of a marine predator, Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 46:1904–1913.

Ross, S. T.
1986. Resource partitioning in fish assemblages: a review of field studies. Copeia 1986:352–388.

Ruiz, G. M., A. H. Hines, and M. H. Posey.
1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Mar. Ecol. Prog. Ser. 99:1–16.

Sale, P. F.
1979. Habitat partitioning and competition in fish communities. *In* R. Stroud and H. Clepper (eds), Predator-prey systems in fisheries management, p. 323–331. Sport Fishing Inst. Wash., D. C.

Schluter, D.
1994. Experimental evidence that competition promotes divergence in adaptive radiation. Science 266:798–801.

Sinclair, A.
1992. Fish distribution and partial recruitment: the case of eastern Scotian Shelf cod. J. Northwest Atl. Fish. Sci. 13:15–24.

Smith, P. W., and L. M. Page.
1969. The food of spotted bass in streams of the Wabash River drainage. Trans. Am. Fish. Soc. 98:647–651.

Stearns, S. C.
1992. The evolution of life histories. Oxford Science Publ., Oxford, 264 p.

Stefanescu, C., J. Rucabado, and D. Lloris.
1992. Depth-size trends in western Mediterranean demersal deep-sea fishes. Mar. Ecol. Prog. Ser. 81:205–213.

Stergiou, K. I., and D. A. Pollard.
1994. A spatial analysis of the commercial fisheries catches from the Greek Aegean sea. Fish. Res. 20:109–135.

Swain, D. P.
1993. Age- and density-dependent bathymetric pattern of Atlantic cod (*Gadus morhua*) in the Southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 50: 1255–1264.

Tanaka, M.
1985. Factors affecting the inshore migration of pelagic larval and demersal red sea bream *Pagrus major* to a nursery ground. Trans. Am. Fish. Soc. 114:471–477.

Tremblay, M. J., and M. Sinclair.
1985. Gulf of St. Lawrence cod: age-specific geographic distributions and environmental occurrences from 1971 to 1981. Can. Tech. Rep. Fish. Aquat. Sci. 1387, 43 p.

Tsimenides, N., G. Tserpes, A. Machias, and A. Kallianiotis.
1991. Distribution of fishes on the Cretan shelf. J. Fish Biol. 39:661–672.

Vassilopoulou, V., and C. Papaconstantinou.
1992. Age growth and mortality of the red porgy, *Pagrus pagrus*, in the eastern Mediterranean sea (Dodecanese, Greece). Vie Milieu 42:51–55.

Vaughan, D. S., G. R. Huntsman, C. S. Manooch, F. C. Rohde, and G. F Ulrich.
1992. Population characteristics of the red porgy, *Pagrus pagrus*, stock off the Carolinas. Bull. Mar. Sci. 50:1–20.

Wallace, R. K., Jr.
1981. An assessment of diet-overlap indexes. Trans. Am. Fish. Soc. 110:72–76.

Werner, E. E.
1979. Niche partitioning by food size in fish communities. *In* R. Stroud and H. Clepper (eds), Predator-prey systems in fisheries management, p. 311–322. Sport Fishing Inst. Wash., D.C.

Werner, E. E., and J. F. Gilliam.
1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. 15:393–425.

Werner, E. E., J. F. Gilliam, F. Hall, and G. G. Mittelbach.
1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540–1548.

Werner, E. E ,and D. J. Hall.
1988. Ontogenetic habitat shifts in bluegill: the foraging-predation risk trade-off. Ecology 69: 1352–1366. Biostatistical analysis, 2nd ed. Prentice-Hall, Englewood Cliffs, NJ, 718 p.

Nearshore hardbottom fishes of southeast Florida and effects of habitat burial caused by dredging

Kenyon C. Lindeman
Division of Marine Biology and Fisheries,
Rosenstiel School of Marine and Atmospheric Science,
University of Miami
4600 Rickenbacker Cswy., Miami, Florida 33149
E-mail address (for K. C. Lindeman): klindeman@rsmas.miami.edu

David B. Snyder
Continental Shelf Associates, Inc.
759 Parkway St.
Jupiter, Florida 33477

Abstract.—Fish assemblages of nearshore hardbottom habitats of southeast Florida were quantified at three sites from April 1994 to June 1996. Random 2×15 m transects were visually censused within two replicate areas at each site. The hardbottom at one site was buried by a dredge project to widen a beach one year into the study. A total of 394 transects were sampled. Eighty-six taxa (77 identified to species) from 36 families were censused. Grunts (Haemulidae) were the most diverse family (11 species), followed by the wrasses (Labridae) and parrotfishes (Scaridae) with seven and six species, respectively. The most abundant species were sailors choice (*Haemulon parra*), silver porgy (*Diplodus argenteus*), and cocoa damselfish (*Stegastes variabilis*) with mean abundances (individuals/transect) of 4.5, 3.8, and 3.7, respectively. Early life stages (newly settled, early juvenile, and juvenile) represented over 80% of the individuals at all sites. Newly settled stages of over 20 species were observed in association with hardbottom reef structure. Outside of lagoons, nearshore hardbottom areas are the primary natural structures in shallow waters of mainland Florida's east coast and were estimated to have nursery value for 34 species of fishes. After one year, burial of approximately five ha of hardbottom habitat at one site lowered the numbers of individuals and species by over 30× and 10×, respectively. Due to their early ontogenetic stage, many of these species may not be adapted for high mobility in response to habitat burial. Dredging effects may be amplified by burial prior to and during spring and summer periods of peak larval recruitment.

Manuscript accepted 28 August 1998.
Fish. Bull. 97:508–525 (1999).

The southeast coast of mainland Florida is within a biogeographic transition zone of high marine biodiversity (Briggs, 1974; Gilmore, 1995). This region is also undergoing some of the most rapid human population growth of any area of the United States (Culliton et al., 1990). Due to the economic and recreational value of beaches, substantial marine dredging projects (up to 1.5×10^5 m^3 of fill/project) are commony used to widen beaches that are subject to erosion in the area (ACOE, 1996). Nearshore hardbottom habitats are the primary natural reef structures of this region at depths of 0–4 m and are often buried or indirectly affected by these projects. To date, no quantitative studies of the fish fauna of these habitats or the effects of beach dredge-and-fill projects on nearshore fishes are available (NRC, 1995).

Nearshore hardbottom habitats of this area are derived from accretionary ridges of coquina mollusks, sand, and shell marl which lithified parallel to ancient shorelines during Pleistocene interglacial periods (Duane and Meisburger, 1969; Hoffmeister, 1974). The habitat complexity of these limestone structures has been expanded by colonies of tube-building polychaete worms (Kirtley and Tanner, 1968) and other invertebrate and macroalgal species (Goldberg, 1973; Nelson, 1989; Nelson and Demetriades, 1992). In southeast Florida, most nearshore hardbottom structures are within 200 m of the shore. These habitats are often centrally located between mid shelf reefs to the east and estuarine habitats within inlets to the west. Therefore, they may serve as settlement habitats for immigrating larvae or as intermediate nursery habitats for juveniles emigrating out of inlets (Vare, 1991; Lindeman, 1997a). Nonetheless, most administrative reviews have concluded that the fish habitat value of nearshore hardbottom and the effects of dredge-based beach restoration projects are minimal (e.g. ACOE, 1996).

This study quantifies nearshore hardbottom fish assemblages on the southeast coast of mainland Florida over a 27-month period. The effects of dredge-fill placement were also examined because the hardbottom habitat at one site was buried on account of a beach restoration project 12 months into the study. Three primary objectives were examined. First, spatial and temporal attributes of fish assemblages at

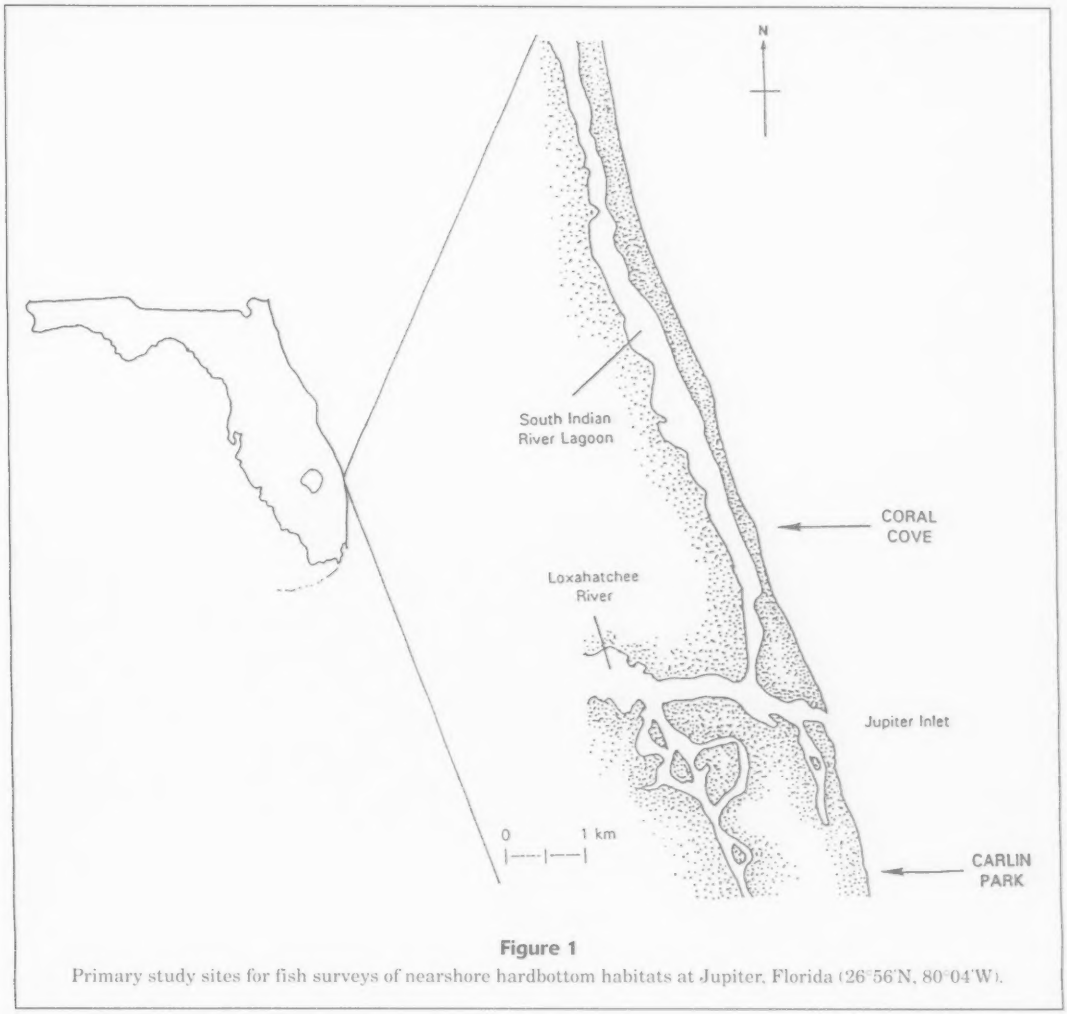


Figure 1

Primary study sites for fish surveys of nearshore hardbottom habitats at Jupiter, Florida (26°56'N, 80°04'W).

three undisturbed hardbottom sites were characterized. Second, abundances of different life stages were compared to assess the potential nursery value of nearshore hardbottom habitat. Third, effects of dredge burial on numbers of individuals and species were compared between a site subjected to burial and a control site.

Methods

Study areas

Fish abundances were quantitatively surveyed on two nearshore hardbottom sites approximately 2 km north (Coral Cove) and 2 km south (Carlin Park) of Jupiter Inlet, Florida (26°56'N, 80°04'W) from April 1994 through June 1996 (Fig. 1). Sampling at both sites extended approximately 100 m offshore to a depth of 4 m. Nearshore hardbottom of similar depth and structure at Ocean Ridge, immediately south of the South Lake Worth Inlet (26°31'N, 80°02'W) was also surveyed for comparative purposes during the summer of 1995.

Weathered limestone outcroppings were common between depths of 0 and 4 m at all sites. These structures have a variety of names (e.g. *Anastasia* formation outcroppings, coquina reefs, worm reefs) but are referred to by their most common name, "nearshore hardbottom," in the present study. In some areas, the hardbottom extended 1.75 m above the bottom and was highly convoluted. Shoreward portions of the hardbottom were exposed at low tide. Epibiota consisted of a variety of invertebrates and algae. The

most widespread encrusting organism was the reef-building sabellariid worm *Phragmatopoma lapidosa* (=*P. caudata*; Kirtley, 1994), often covering over 50% of the hardbottom at all sites.

A beach restoration project occurred at Carlin Park in March and April of 1995. More than 350,000 m^3 of beach-compatible sediments were excavated by a cutter-head dredge from a site 0.8 km offshore and hydraulically pumped along 1.8 km of shoreline. Bulldozers extended the fill seaward to an estimated width of 60 m. An estimated total of 4.9 to 5.7 ha (12–14 acres) of nearshore hardbottom was buried.[1] Visual surveys of fishes were conducted for 12 months before burial and 15 months after burial at both Carlin Park (the impact site) and Coral Cove (the control site). Little or no hardbottom was observed in fish surveys at Carlin Park after the project.

Survey protocol

During each site visit, three to five transects within two adjacent areas (=6–10 total transects/site) were censused. These 2 × 15 m transects were randomly located at depths ranging from one to four m. Transects were deployed along random compass headings at random distances between successive transects. Random number tables were used prior to site visits to determine the compass headings and distances between transects (based on numbers of fin kicks). All fishes observed within one m of each side of the transect line were identified and tallied by a snorkeler. The survey zone extended from the bottom to the surface and 2 m in front of the observer. Ledges and sand-rock interfaces were examined for fishes. Rocks were not overturned. The proportion of hardbottom to sand was estimated within each transect. An estimated 35% of the area within all transects was sand. Surveys were conducted between 0900 and 1700 and avoided twilight periods. To compare fish abundances at hardbottom and sand areas, identical transect methods were used at nearshore sand plains greater than 50 m from any hardbottom structures.

Monthly visual censusing occurred from April 1994 to June 1996 as permitted by nearshore visibility and sea state. Discharges of turbid water from Jupiter Inlet and wave resuspension of fine sediments sometimes resulted in turbidity levels that precluded sampling. Samples were obtained for all months except October through January when waves and turbidity were typically prohibitive.

[1] Davis, P. 1998. Palm Beach County Department of Environmental Resources Management, 3323 Belvedere Rd., Bldg. 502, W. Palm Beach, FL 33406. Personal commun.

In addition to total abundances, early life stages were also enumerated. Fork length was used for size estimation. Following Lindeman (1986; 1997a), life stages of grunts (*Haemulon* and *Anisotremus*) were recorded as follows: newly settled (<2 cm), early juvenile (2–5 cm), juvenile (5–15 cm), and adult (>15 cm). For other families, the same newly settled size range (<2 cm) was used. The early juvenile designation was used only for grunts because of the distinct morphological features of the 2–5 cm size range (Lindeman, 1986). Juvenile and adult stages were based on size and pigment patterns reported in the literature (e.g. Robins and Ray, 1986; Humann, 1994). Species identifications of the newly settled or juvenile stages for certain taxa were limited by very similar morphological features (e.g. scarids, kyphosids, gerreids, haemulids, clupeids). Some early stage identifications were therefore recorded only at the genus or family level. Collections of small schools of newly settled grunts were made with hand nets at both Jupiter sites in 1994 and 1995 to supplement field identifications. All collections were deposited at the Florida Museum of Natural History, University of Florida.

Data analyses

To address the first objective of our study, two complementary multivariate methods were used to spatially and temporally characterize the assemblages at the three sites. The second objective was addressed by univariate testing of the hypothesis that abundances of different life stages would not differ significantly within sites. The third objective was examined with the hypothesis that numbers of individuals and species would not differ significantly between an impact site where allmost all the hardbottom was buried and a control site that was unaffected by the burial. In univariate analyses, data were standardized as the mean number of individuals per transect and as the mean number of species per transect.

Samples were temporally unbalanced owing to the inability to visually sample during portions of the winter. Therefore, to examine the first objective, multivariate ordination and classification (cluster analysis) of a samples-by-taxa matrix for the entire, unpooled data set were used. These analyses were performed on a data set of 31 samples (16 from Coral Cove, 12 from Carlin Park, and 3 from Ocean Ridge) and 61 taxa. Each sample represented a site visit where 6 to 10 transects were censused. Samples from Carlin Park did not include postdredging site visits because these samples contained few or no fishes. The 61 taxa were those remaining from a total of 86 after eliminating taxa occurring only once across all

samples. Within each sample, counts for individual taxa were averaged over all transects to provide values for the matrix. These values were log-transformed [$\log_{10}(n+1)$] to prevent abundant taxa from dominating the ordination or classification results.

The transformed matrix was analyzed by correspondence analysis (CA), a method that employs a two-way weighted averaging algorithm to produce simultaneous ordination of sites and taxa (Gauch, 1982; Jongman et al., 1995). These analyses were performed with the program CANOCO (ter Braak, 1988). From the same log-transformed data matrix, normal (samples) and inverse (taxa) resemblance matrices were generated by using the Bray-Curtis dissimilarity index (Bray and Curtis, 1957). Normal and inverse resemblance matrices were clustered separately by the unweighted paired-group method of averaging (UPGMA) (Sneath and Sokal, 1973). All dissimilarity and cluster analyses were computed with NTSYS-pc software (Rohlf, 1997).

To address the second project objective, numbers of life stages per transect were compared within each site. Data were analyzed by using a parametric one-way ANOVA when variances were homogeneous (Bartlett's test). *A posteriori* comparisons of differences among means employed Tukey's HSD test. Variances of numbers of life stages of grunts per transect at the two Jupiter sites remained heterogeneous after $\log_{10}(n+1)$ transformation and a Kruskall-Wallis non parametric, single classification ANOVA was used. Probability was calculated using the χ^2 approximation. Two-sample t-tests for unequal variances were used to compare numbers of individuals at hardbottom and natural sand sites. Only hardbottom samples from months when natural sand sites were sampled (March and April 1995) were used for these tests. In all statistical tests, differences were considered significant at $P<0.05$.

The third objective, examining dredging effects at the impact site (Carlin Park) and the control site (Coral Cove), employed a BACIPS (before after control impact paired series) design (Stewart-Oaten et al., 1986; Osenberg and Schmitt, 1996). This approach compares differences in variables between sites over time before and after the impact. The differences in the paired series were examined by two-sample t-tests by using the mean number of both individuals and species as the variables (Stewart-Oaten, 1996).

Results

A total of 352 transects was sampled at the two Jupiter sites: 204 at Carlin Park and 148 at Coral Cove.

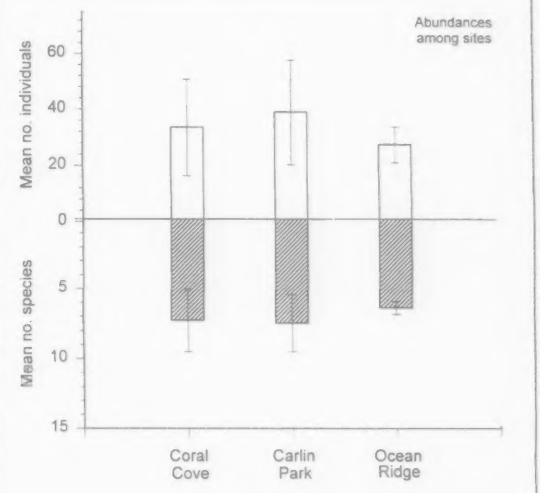


Figure 2

Mean number of individuals and species per transect (with 95% confidence intervals) for all nearshore hardbottom sites. Only predredging data were used for Carlin Park site. Sample sizes: Coral Cove: 148 transects; Carlin Park: 112; Ocean Ridge: 36.

At Carlin Park, 112 transects were sampled before burial and 92 after. At Coral Cove, 58 transects were sampled before the burial of the Carlin Park reef and 90 after. Eight transects were sampled over natural sand habitats at Carlin Park and six at Coral Cove. An additional 36 hardbottom and 6 sand transects were sampled at Ocean Ridge.

Family and species abundances

Thirty-six families of fishes were censused among the three hardbottom sites. The most speciose family was the grunts and margates (Haemulidae) with 11 species of *Haemulon* and *Anisotremus*. The wrasses, parrotfishes, and damselfishes (Labridae, Scaridae, and Pomacentridae) had seven, six, and five species, respectively. Four species each of jacks (Carangidae), snappers (Lutjanidae), and clinids (Labrisomidae) were recorded. These seven families contained 50% of the total species censused. Eighty-six taxa (77 identified to species) and 10,491 individuals were censused at all sites (Appendix). At Coral Cove, 64 species and 5093 individuals were recorded. At Carlin Park, 53 species and 4438 individuals were recorded. At Ocean Ridge, 48 species and 960 individuals were recorded. Mean numbers of both species and individuals per transect were similar among all sites (Fig. 2).

Table 1

Mean number of individuals/transect and frequency of occurrence for the most abundant three families, genera, and species at all nearshore hardbottom sites. Only predredging data were used for Carlin Park site. CC: Coral Cove (148 transects); CP: Carlin Park (112 transects); OR: Ocean Ridge (36 transects); GM: grand mean.

	Mean number/transect				% frequency occurrence			
	CC	CP	OR	GM	CC	CP	OR	GM
Family								
Haemulidae	15.5	17.4	9.4	15.5	89	90	92	90
Pomacentridae	5.9	7.9	5.7	6.6	81	95	86	87
Sparidae		5.9	3.7	3.9		37	44	38
Labridae	3.2			3.0	65			64
Genus								
Haemulon	9.8	15.3	6.2	11.4	75	80	42	75
Stegastes	3.4	6.1		4.3	72	89		73
Anisotremus	5.7		3.2	4.1	74		39	69
Diplodus		5.8	3.7	3.8		35	36	65
Species								
Haemulon parra	4.4	5.0	3.4	4.5	62	64	33	59
Diplodus argenteus		5.8	3.7	3.8		35	36	36
Stegastes variabilis		5.4		3.7		86		71
Labrisomus nuchipinnis	3.1			2.7	73			69
Abudefduf saxatilis			3.1	2.3	17			31
Anisotremus surinamensis	3.5			2.2			36	43

The three most abundant species were the sailors choice (*Haemulon parra*), silver porgy (*Diplodus argenteus*), and cocoa damselfish (*Stegastes variablis*) with means of 4.5, 3.8, and 3.7 individuals/transect over all sites (Table 1). The most abundant species at Coral Cove, sailors choice, black margate (*Anisotremus surinamensis*), and hairy blenny (*Labrisomus nuchipinnis*), represented 32% of all individuals. Seven of the 15 most abundant species at Coral Cove were grunts. At Carlin Park, silver porgy, cocoa damselfish, and sailors choice represented 41% of all individuals. Eight of the 16 most abundant species were grunts. At Ocean Ridge, the most abundant species were silver porgy, sergeant major (*Abudefduf saxatilis*), and sailors choice. Grunt species ranked first in frequency of occurrence per transect at Coral Cove and Ocean Ridge, and second at Carlin Park (Table 1). Damselfish species ranked first in frequency at Carlin Park and second at the other sites. The most frequently occurring species overall were cocoa damselfish, hairy blenny (*Labrisomus nuchipinnus*), and sailors choice (Table 1).

Normal cluster analysis of samples from all sites resolved three groups that broadly reflected temporal patterns (Fig. 3). No distinct spatial groupings emerged in the normal analysis. Group 1 consisted of 21 samples (eight from Carlin Park, ten from Coral Cove, and three from Ocean Ridge) mostly taken in spring and summer months. Group 2 consisted of 8 samples (four each from Carlin Park and Coral Cove) taken in mid and late summer. Group 3 included the only winter samples (February 1995 and 1996) taken during the project.

Inverse cluster analysis revealed seven groups of taxa (Fig. 4). Group A contained 26 common taxa including the most frequently occurring and abundant species from visual surveys such as sailors choice, cocoa damselfish, hairy blenny, and silver porgy (Table 1). This group characterized the spring-summer group of samples defined by normal group 1. The remaining six groups consisted of taxa that were temporally variable in their abundance and occurrence in the samples. Group B was characterized by species that occurred at lower abundances. Groups F and G were represented by single taxa: *Apogon maculatus* and *Archosargus probatocephalus*, respectively. The latter species was important in defining normal group 3 (Fig. 3).

Ordination of samples projected on CA axes 1 and 2 produced a pattern that generally agreed with the normal cluster analysis (Fig. 5A). The eigenvalue for CA axis 1 was 0.218 and accounted for 16.9% of the

variation in the data set, whereas the eigenvalue for CA axis 2 was 0.124 and accounted for 9.7% of the variation in the data set. Samples from August and September at Coral Cove and Carlin Park separated from all other samples along CA axis 1. In general, samples were not spread widely along CA axis 2; however, two samples, May 1995 at Ocean Ridge and February 1995 at Carlin Park, did separate from the other sites.

The ordination of taxa on CA axes 1 and 2 showed how the taxa were distributed in relation to the hardbottom samples along these same axes (Fig. 5B). The most common species (e.g. Table 1) clustered near the origin of the ordination. Taxa with high scores along CA axis 1 included infrequently occurring species such as *Halichoeres poeyi*, *Haemulon aurolineatum*, *Mulloidichthys martinicus*, and *Caranx ruber*. Low scores on CA axis 1 were *Echidna catenata*, *Acanthurus chirurgus*, *Chaetodon ocellatus*, and Sciaenidae sp. Species with high scores on axis 2 were *Sparisoma aurofrenatum*, *Chaetodon ocellatus*, and *Sparisoma viride*. These were most abundant at Ocean Ridge in May 1995 and were responsible for the separation of this sample from all others along CA axis 2.

In comparisons of hardbottom and natural sand, 20 transects over natural sand plains recorded only four taxa. The clupeid, *Harengula jaguana*, was most abundant (18 juveniles in two schools total). An unidentified *Eucinostomus* species, *Gerres cinereus*, and *Caranx bartholomaei* were also recorded (four, one, and one individuals, respectively). Hardbottom habitats typically had over thirty times the individuals per transect as natural sand habitats. Two-sample *t*-tests comparing hardbottom with sand habitats rejected the hypothesis of no differences in mean numbers of individuals per transect ($P<0.005$).

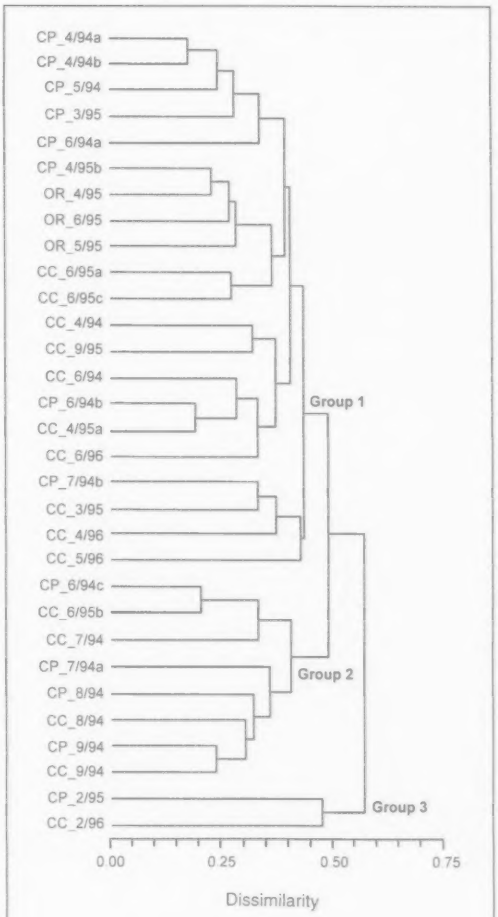


Figure 3

Clustering of visual census samples (sites and times) by UPGMA analysis of a normal Bray-Curtis dissimilarity matrix. CC: Coral Cove; CP: Carlin Park; OR: Ocean Ridge.

Life-stage abundances

At all sites, juveniles were the most abundant life stage among the top ten species (Table 2). At the two intensively sampled sites in Jupiter, the numbers of juveniles of all species pooled were significantly greater than any other life stage (ANOVA, $P<0.01$, Tukey's HSD). There were no significant differences in abundances among newly settled, early juvenile, and adult stages (Tukey's HSD). At both Jupiter sites, at least 80% of the individuals were early life stages (pooled newly settled, early juvenile, and juvenile stages)(Fig. 6). Abundances of newly settled and early juvenile stages at Ocean Ridge were similar to the Jupiter sites (Table 2), although numbers of juveniles and adults were lower. Newly settled stages of over 20 species were recorded on nearshore hardbottom structures among the three sites.

Eight of the ten most abundant taxa by site were represented primarily by early stages (Table 2). Cocoa damselfish and hairy blenny occurred most abundantly as adults. Adults of at least five of the top ten species occurred as residents, not transients. These included sergeant major, hairy blenny, cocoa damselfish, silver porgy, and black margate. Adults of a variety of less common species occurred but were often less abundant than early life history stages. Newly settled and juvenile stages often appeared to display more site-fidelity with hardbottom structure than did adults.

Six species of grunts (four *Haemulon* and two *Anisotremus*) and two species of damselfishes (*Stegastes*

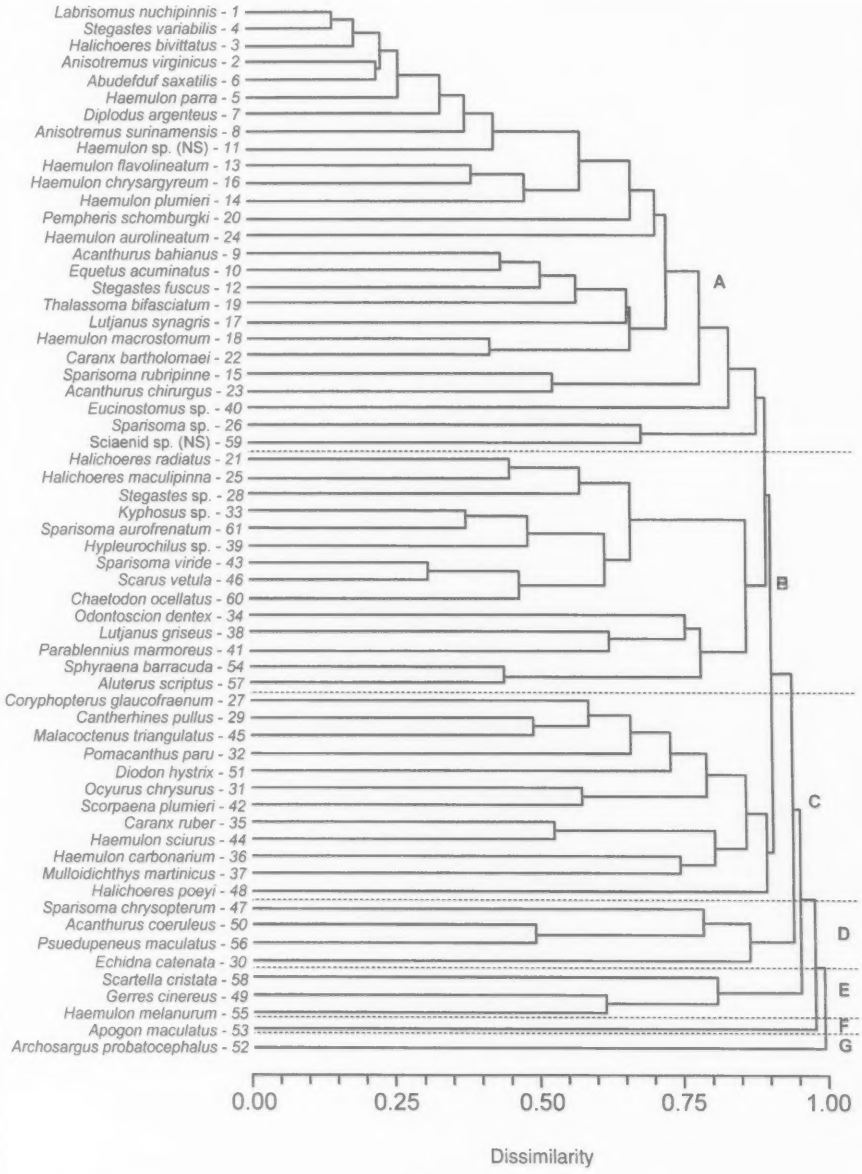


Figure 4

Clustering of fish taxa co-occurrence at three nearshore hardbottom sites by UPGMA analysis of an inverse Bray-Curtis dissimilarity matrix. Numeric codes used in correspondence analysis are next to each name. NS: Newly Settled. Dashed lines delineate groups A–G.

and *Abudefduf*) ranked within the ten most abundant species from all three sites (Table 2). Relative abundances of the life stages of all grunts censused at the Jupiter sites are shown in Figure 7. Early juvenile stages of the most abundant species, sailors choice, were significantly more abundant than any other life stage at each of the three sites (Kruskal-Wallis ANOVA, $P<.001$, and *a posteriori* pairwise comparisons). Adult sailors choice were significantly lower in abundance than juvenile stages (Kruskal-Wallis ANOVA, $P<0.001$). Black margate and porkfish, *Anisotremus virginicus*, ranked second and

Table 2

Mean number of individuals/transect by life stage for the ten most abundant taxa at each of three sites. NS: Newly Settled; EJ: Early Juvenile (for haemulids only); J: Juveniles; A: Adults. Only predredging data were used for Carlin Park site. na = not available.

	Mean number individuals/transect											
	Coral Cove				Carlin Park				Ocean Ridge			
	148 transects				112 transects				36 transects			
Species	NS	EJ	J	A	NS	EJ	J	A	NS	EJ	J	A
Haemulon parra	0.7	2.7	0.8	0.2	0.7	3.8	0.8	0.1	0.4	2.6	0.4	<0.1
Diplodus argenteus	0.3	na	1.7	0.3	1.6	na	4.1	0.1	0.7	na	2.8	0.2
Stegastes variabilis	0.2	na	1.4	1.3	0.4	na	1.4	3.5	0.4	na	0.9	0.6
Halichoeres bivittatus	0.2	na	2.3	0.5	0.3	na	2.1	0.5	0.3	na	1.1	<0.1
Labrisomus nuchipinnis	0	na	0.8	2.3	0	na	0.3	2.0	<0.1	na	0.5	1.8
Abudefduf saxatilis	0.4	na	2.0	0.1	0.3	na	1.1	0.4	1.3	na	1.7	0.1
Anisotremus surinamensis	0.4	1.9	1.1	0.1	0.1	0.3	0.3	0	0.5	0.6	0.4	0
Anisotremus virginicus	0.9	0.7	0.4	0.2	0.3	0.9	0.3	<0.1	0.9	0.2	0.4	0.3
Haemulon aurolineatum	0	0.7	1.0	0	0	0.1	2.5	0	0	0	0	0
Haemulon sp.	1.8	<0.1	0	0	2.1	<0.1	0	0	0.9	0	0	0
Haemulon flavolineatum	<0.1	0.6	0.3	<0.1	0	0.9	1.0	<0.1	0	1.1	0.1	0
Haemulon chrysargyreum	0	<0.1	0.3	0	<0.1	0.3	1.7	0	0	0	0	0
Total means of life stages per site	4.9	6.6	12	5.0	6.3	6.3	15.5	6.6	5.0	5.4	7.4	3.0

third in overall abundance among grunts and were represented by all life stages (Fig. 7). Tomtate, *Haemulon aurolineatum*, ranked fourth on the basis of large but infrequent influxes of early stages. Outside of these pulses, tomtate was not an abundant or frequently occurring species at any site during any life stage.

Some newly settled grunts could not be positively identified during visual surveys and were pooled as *Haemulon* sp. (newly settled larvae of *Anisotremus* are distinctive, Lindeman, 1997a). This group contained epibenthic larvae of several species and ranked tenth in abundance among all taxa (Table 2) and fifth among haemulids (Fig. 7). The largest component of these unidentified schools was probably sailors choice. This assumption is based on 1) the greater relative abundances of sailors choice early juveniles at all sites; 2) the close proximity of sailors choice early juveniles to these newly settled *Haemulon* sp.; and 3) collections of several newly settled *Haemulon* sp. schools most commonly contained sailors choice upon microscopic examination.

Early stages of commercially valuable species occurred infrequently during the surveys, although recreationally important species were common. The most abundant commercial family at the nearshore hardbottom sites was the Lutjanidae (snappers). Four snapper species, totaling 58 individuals, were recorded at all sites. Thirty-eight of these were lane snapper, *Lutjanus synagris*. Thirty-three of these were juveniles, the majority less than five cm. Five newly settled individuals (<2 cm) were also recorded. Ten yellowtail snapper, *Ocyurus chrysurus*, were recorded, nine small juveniles and one newly settled individual. Unlike grunts, newly settled and small juvenile snappers were not gregarious, occurring individually or in pairs near interfaces of hardbottom structure and sand. Gray snapper, *Lutjanus griseus*, and schoolmaster, *Lutjanus apodus*, occurred only as older juveniles or adults and in low numbers (eight and two individuals, respectively).

Comparisons of interannual and seasonal patterns of life stage abundances were limited by temporally unbalanced sampling. Wind and wave conditions from September through February made collection of nearshore visual data in fall and winter erratic or impossible. Several hurricanes during July and August of 1995 produced wave and turbidity conditions that interrupted summer sampling as well. Other phenomena, including high winds and discharges of turbid water from the Jupiter Inlet, also precluded sampling for extended intervals. Nonetheless, samples were obtained from Coral Cove (the control site) for three consecutive years for the months of April and June. Comparisons of both numbers of spe-

cies and numbers of individuals per transect for April among 1994–96 revealed no significant interannual differences (ANOVA, P=0.34; ANOVA, P=0.21). Identical comparisons for June among the same three-year period revealed no differences among mean numbers of individuals (ANOVA, P=0.06), but significant differences among numbers of species (ANOVA, P<0.05). Pairwise comparisons using Tukey's HSD showed that Coral Cove in June 1995 had significantly more species than in June 1996 (mean species numbers: 8.7 versus 5.3).

Seasonal occurrence of only newly settled stages was examined at Coral Cove (Fig. 8). The timing and abundance of species occurrences suggested seasonal variations with peaks of newly settled stages in late spring and early summer. Sizes and numbers of individuals typically increased as summer progressed. Abundances of early stages for most species appeared to be low in February and March prior to peak spawning activity for many species (García-Cagide et al., 1994). However, difficulties in the collection of visual surveys constrained the examination of fall and winter patterns.

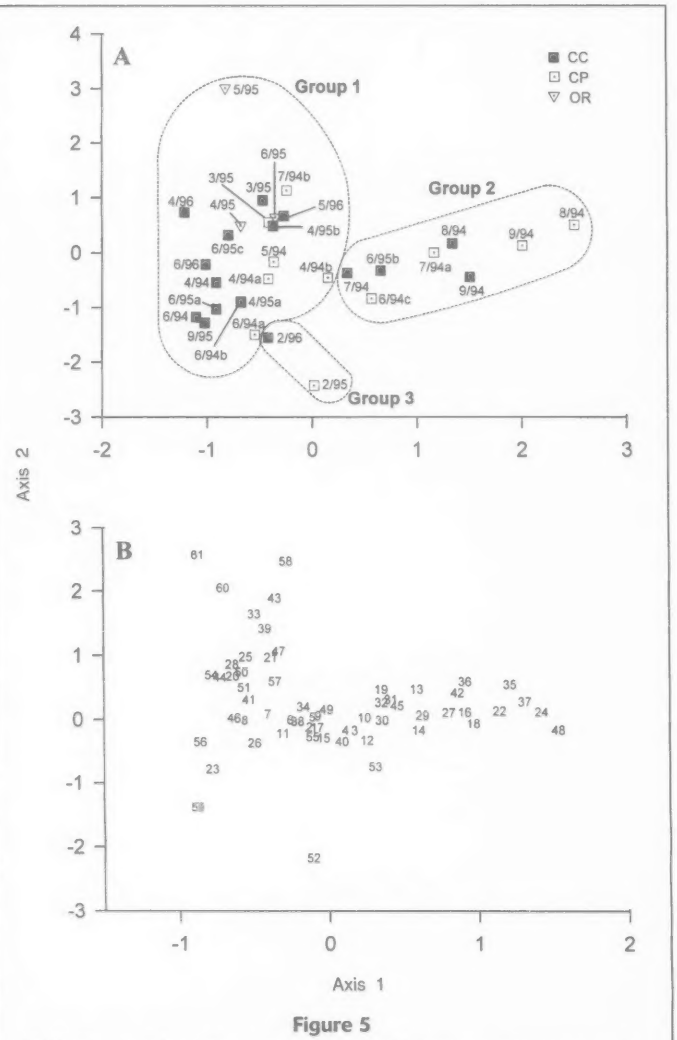


Figure 5

(A) Ordination of sample scores on axes 1 and 2 from correspondence analysis of a samples by taxa matrix of census data from Coral Cove (CC), Carlin Park (CP), and Ocean Ridge (OR). Groups 1–3 from Figure 3. **(B)** Ordination of taxa scores from the same correspondence analysis. Numeric codes for taxa are given in Figure 4.

Ichthyofaunal characteristics after habitat burial

Prior to habitat burial, fish assemblages at the two Jupiter sites were similar in species composition and relative abundance (Figs. 2, 3, and 5A). Pre- and postburial numbers of individuals and species at the control and impact sites are plotted in Figure 9. The hypotheses of no differences in total numbers of individuals and species before and after dredge burial of hardbottom were both rejected (P<0.001) in two sample t-tests for equal variances following a BACIPS design (Stewart-Oaten et al., 1986; Osenberg and Schmitt, 1996).

No fishes or exposed hardbottom were recorded in the first postdredging surveys at Carlin Park (13 April 1995). Several hardbottom outcroppings (1 m high by 3 m wide), parallel to the shore, were exposed at a depth of 1.5 to 2.5 m at the site during the second postdredging surveys on 24 April. Two of ten transects crossed narrow outcrops with dense schools of newly settled stages of three grunt species and one drum species (Sciaenidae). Before burial of the reef by extension of the beach width by approximately 60 m, such outcrops were deeper and further offshore than the original hardbottom sampling area. Small outcrops were still present in May and were occupied in two of ten transects by three species of grunts and one damselfish (Fig. 9). Schools of newly settled stages predominated. Such outcrops were not encountered during the 20 surveys in June, and no fishes were present with the exception of several round scad, *Decapterus punctatus*. Ten

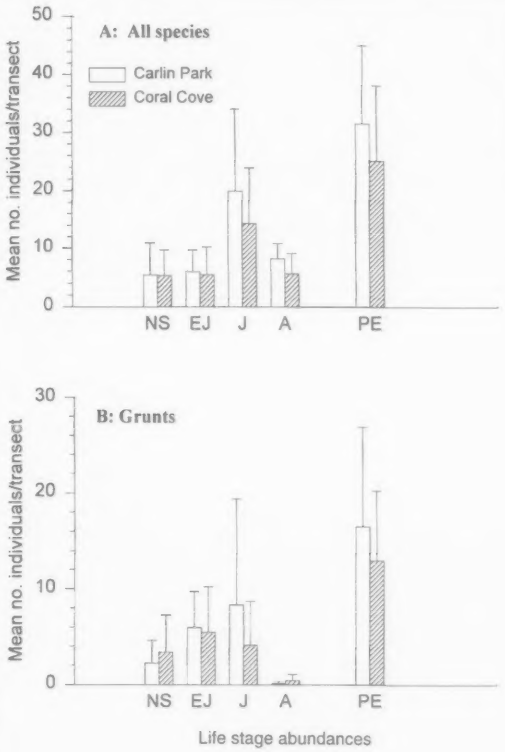


Figure 6

Abundances of different life history stages at the Jupiter hardbottom sites (with 95% confidence intervals). A: All species pooled. B: Pooled grunt species only. Only predredging data were used for Carlin Park site. NS: Newly Settled; EJ: Early Juvenile (for grunts only); J: Juveniles; A: Adults; PE: Pooled Early Stages (=NS+EJ+J).

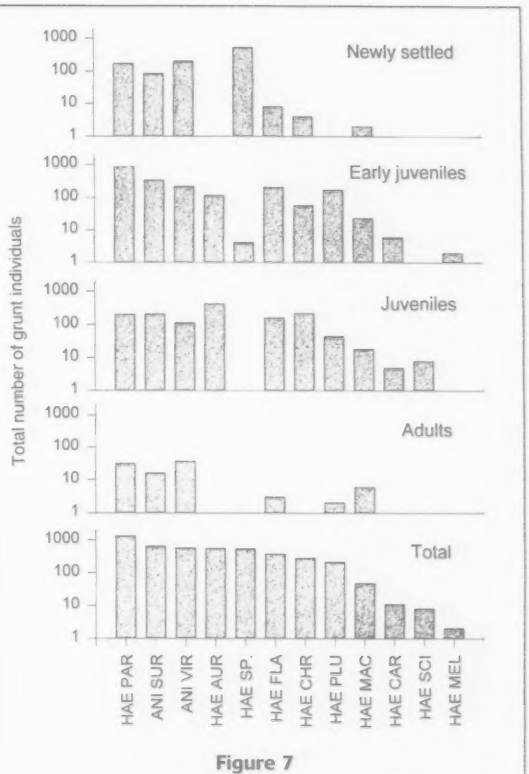


Figure 7

Comparative abundances of grunts among 12 taxa and 4 life history stages. Data pooled from all Coral Cove surveys and predredging Carlin Park surveys (260 transects total). Species represented by abbreviated genus and species names.

surveys in September 1995 recorded no exposed outcrops or fishes. During the following winter, erosion occurred and the width of the new beach was reduced. Some outcrops were re-exposed by the loss of dredgefill. However, wind and waves prohibited visual sampling during this period. Surveys in February, April, and May of 1996 (22 transects total) recorded no species (Fig. 9).

Discussion

Fish assemblages of nearshore hardbottom

The diversity of fishes utilizing nearshore hardbottom habitats of mainland Florida has not been quantified. Qualitative studies by ichthyologists experienced with the substantial taxonomic problems within these diverse, largely juvenile assemblages are also lacking. Three studies have included sections on nearshore hardbottom fishes as part of larger project goals. Gilmore (1977) listed 105 species in association with "surf zone reefs" at depths less than two m. Two additional species were added in later papers (Gilmore et al., 1983; Gilmore, 1992). Using visual surveys, Vare (1991) recorded 118 species from nearshore hardbottom sites in Palm Beach County. Futch and Dwinell (1977) included a list of 34 species obtained from several ichthyocide collections on "nearshore reefs." Including species from these prior studies, 192 species have now been recorded in association with nearshore hardbottom habitats of mainland southeast Florida (Table 3.3 in Lindeman, 1997a). Numbers of labrisomid, blenniid, gobiid, and apogonid species may be underestimated owing to their small size or cryptic behaviors. Other hardbottom habitats of the southeast United States occur in areas with substantially different physi-

ographic regimes (Sedberry and Van Dolah, 1984; Chiappone and Sullivan, 1994) and may show differing patterns of fish diversity.

Spatial and temporal attributes of fish assemblages at the three sites in the present study were examined by using ordination and cluster analysis. Visual census samples collected from March through July were similar in species composition and relative abundance among sites (Fig. 3). This finding is in agreement with the similar plots of individual and species abundances among sites (Fig. 2). The relative homogeneity of these samples was further reflected in the co-occurrence of many taxa including haemulids (*Haemulon parra*, *H. flavolineatum*, *H. chrysargyreum*, *Anisotremus virginicus*, *A. surinamensis*), pomacentrids (*Stegastes variabilis*, *Abudefduf saxatilis*), labrisomids (*Labrisomus nuchipinnis*), sparids (*Diplodus holbrooki*), labrids (*Halichoeres bivittatus*, *Thalassoma bifasciatum*) and scarids (*Sparisoma rubripinne*) (Fig. 4). With the exception of *L. nuchipinnis* and *S. variabilis*, most taxa occurred as early life stages.

Samples from late summer (August and September) were distinct from the spring and early summer in both cluster analysis and ordination (group 2, Figs. 3 and 5). The only two samples taken in winter (February) differed from all other samples in the analyses (group 3, Figs. 3 and 5). These patterns suggest that some seasonality in assemblage structure existed. This may reflect late spring and summer peaks in larval settlement in contrast to reduced winter settlement and, possibly, influxes of older juveniles from inshore lagoonal habitats. Substantial numbers of many species still settled in late summer but were possibly subject to higher predation from older individuals that settled earlier in the year. Various physical disturbances (e.g. winter cold fronts, summer hurricanes) and biological phenomena (variation in larval recruitment) affect the composition of fish assemblages of nearshore hardbottom. The turbidity generated by physical disturbances constrains the visual surveys needed to assess their immediate effects.

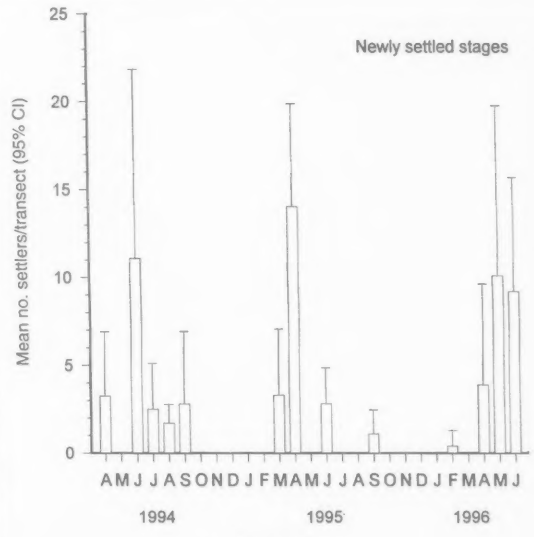


Figure 8

Mean number of newly settled individuals per transect for all species pooled at Coral Cove, 1994-1996 (n =148 transects).

Nursery habitats and nearshore hardbottom

With increasing human modifications of coastal areas, detailed knowledge of habitat usage is a key component of informed fishery and coastal land management. Identification of essential habitats includes the evaluation of spatial distributions of structural habitats across the shelf and habitat requirements of key taxa. Several lines of evidence suggest that nearshore hardbottom habitats along the mainland coast of east Florida can serve as nursery areas for many coastal fish species. Over 80% of the individuals at all sites were early life stages. Eight of the top ten species were consistently represented by early stages. Use of hardbottom habitats was recorded for newly settled stages of more than 20 species. In addition, other natural habitats with substantial vertical relief were absent from the shallow physiographic regimes where nearshore hardbottom occurred.

Although suggestive of nursery value, these lines of evidence need to be viewed in the appropriate context. High abundances of early life stages compared with adults do not guarantee that a habitat is a valuable nursery. High mortality rates in many reef fish populations (Sale, 1980; Shulman and Ogden, 1987; Richards and Lindeman, 1987; Jones, 1991) suggest that early stages will typically be more abundant than adults. If spatial distributions of all life stages are homogeneous, all habitats will have more early stages than adults. However, the abundances of early stages on nearshore reefs probably reflect more than just larger numbers of homogeneously distributed recruits. Newly settled stages of eight of twelve species of grunts and eight of nine species of snappers of the southeast mainland Florida shelf have been recorded primarily in depths less than ten m (Lindeman et al., 1998). Adults of most species are typically uncommon or absent in shallow habitats. There is considerable evidence for cross-shelf habitat seg-

regation among life stages of many grunt and snapper species from other regions as well; early demersal stages appear to most commonly use shallow habitats (Starck, 1970; Dennis, 1992). Similar ontogenetic differences in distribution and abundance exist for many other taxa that utilize nearshore hardbottom habitats.

Determining if the availability of habitat structure limits survival of early stages is important in assessing nursery value. Absences of habitat structure can result in increased predation or lowered growth (Hixon, 1991). In southeast mainland Florida, many natural nearshore marine habitats outside of coastal lagoons and between 25°30'N and 26°20'N (Dade and Broward Counties) are sand plains lacking hardbottom and substantial three-dimensional structure (ACOE, 1996). Although large stretches of nearshore hardbottom exist between 26°20'N and 27°50'N (Palm Beach, Martin, St. Lucie, and Indian River Counties) these habitats are often separated by kilometers of sand plains. There are no other natural habitats in the same nearshore areas that can support equivalent abundances of early life stages. These conditions could promote a demographic bottleneck that limits local adult populations owing to limited habitat availability for early stages.

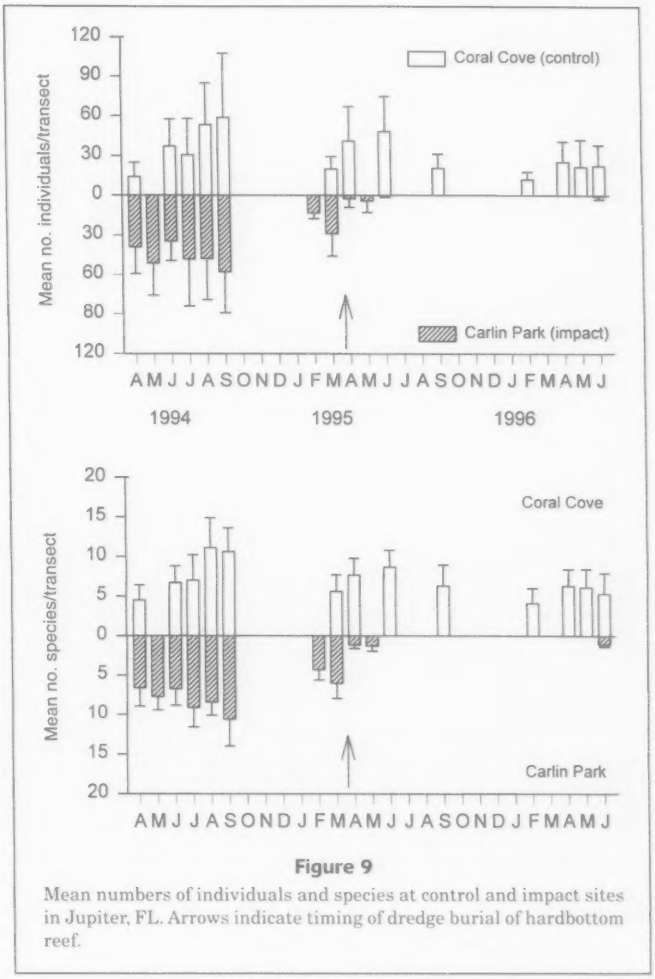


Figure 9

Mean numbers of individuals and species at control and impact sites in Jupiter, FL. Arrows indicate timing of dredge burial of hardbottom reef.

Despite their shallow depth, nearshore hardbottom reefs are positioned within current and tide regimes that can support considerable larval abundances. The occurrence of presettlement larvae in these areas is reflected by the abundances of newly settled stages in the present study and larvae in nearshore zones of Gulf of Mexico barrier islands (Ruple, 1984; Ross et al., 1987). Newly settled individuals were not recorded during any surveys of pure sand habitats in the present study. However, the presence of nearshore hardbottom promoted substantial colonization of shallow outcrops by larvae of many species, including haemulids, lutjanids, sparids, labrids, gerreids, sciaenids, and scarids. Ecotones with high vertical relief (e.g. hardbottom-sand interfaces near ledges) sometimes had large aggregations of newly settled stages of these taxa. However, microhabitat-scale distributions of fishes on nearshore hardbottom remain unquantified.

Use of nearshore hardbottom reefs as nurseries may be bidirectional across the shelf. Both inshore and offshore migrations during differing ontogenetic stages can be facilitated by habitats positioned centrally on the shelf. Nearshore hardbottom may serve a primary nursery role for incoming early life stages that would undergo increased predation mortality without shelter. Nearshore hardbottom may also serve as secondary nursery habitat for juveniles that emigrate out of inlets towards offshore reefs. This pattern is seen in gray snapper and bluestriped grunt which often settle inside inlets and primarily use nearshore hardbottom as older juveniles. In addition, some species use these structures as resident nurseries, settling, growing-out, and maturing sexually as permanent residents (e. g. pomacentrids, labrisomids). A secondary nursery role may also result from increased growth because of higher food availabilities in structure-rich environments. The intermediate cross-shelf positioning and other attributes reviewed above suggest nearshore hardbottom rep-

resents essential fish habitat for many species following NOAA (1996). Bidirectional use of nursery habitats positioned between inshore grassbeds and offshore reefs requires further study.

From abundance patterns of early life stages and the absence of any nearby natural habitats with high vertical relief, nearshore hardbottom of southeast mainland Florida was estimated to have nursery value for 34 species (Appendix). Empirical correlation of variation in early survival with adult population size is an important but rarely achieved component of nursery area evaluation. Combining experimental studies of habitat requirements with broad field surveys can aid in connecting organism-scale attributes with population-scale patterns (Serafy et al., 1997). Early demersal stages of several of the most representative taxa of nearshore hardbottom (e.g. grunt and damselfish species) can be collected and manipulated in the field and laboratory with relative ease (Lindeman, 1986; 1997a). These taxa may serve as useful models for nursery habitat studies that experimentally assess habitat requirements.

Effects of dredge-and-fill activities on ichthyofauna

Burial of the nearshore hardbottom habitat at Carlin Park with dredged sand significantly lowered the abundances of both species and individuals (Fig. 9). Before burial, 54 species were recorded, with mean abundances of 38 individuals and 7.2 species per transect (n=112 transects). After burial, eight species were recorded with mean abundances of less than one individual and species per transect (n=92 transects). No quantitative studies on the effects of nearshore hardbottom burial on fishes are available in the peer-reviewed literature for comparison.

The final supplemental environmental impact statement (EIS) for the Carlin project (Palm Beach Co. Dep. Environ. Resources Management, 1994) summarized several agency and contractor surveys between 1985 and 1990 at Carlin Park. Ten to forty-eight fish species were recorded from qualitative surveys of the hardbottom. Statements regarding the habitat value of nearshore reefs and dredging effects in the Carlin Park EIS emphasized the variable nature of reef exposure and forecast that fish impacts would be minimal and temporary. Primary impacts predicted for fishes were 1) short-term displacement during construction; and 2) temporary loss of food sources. The EIS also emphasized that impacts would be reduced by several features of the project design and nearshore environment. These features included the following: 1) the fishery value of impacted species was low; 2) some amount of hardbottom would remain or would be constructed for mitigation if needed; and 3) construction of the project would take place when fish populations were at their lowest. No mention of direct or indirect mortality upon fishes was made.

The biological assumptions within this EIS are similar to those found in related documents (e.g. ACOE, 1996). For the following reasons, it is suggested that some of these assumptions may be tenuous. The majority of individuals displaced by hardbottom burial in southeast Florida are early stages of economically and ecologically valuable species (Appendix; Figure 9). Early demersal life stages are particularly vulnerable to predators (e.g. Shulman and Ogden, 1987). Displacement was permanent for most individuals because almost all prior habitat was eliminated for at least 15 months (the postburial duration of the present study). Because of behavioral and morphological constraints on flight responses, high mortalities are probably unavoidable for many cryptic species, newly settled life stages, or other site-associated taxa subjected to direct habitat burial (Table 4.10 in Lindeman, 1997a). Whether a fish population is seasonally low at the time a project begins is insignificant if dredging will bury the habitat immediately before the peak period of larval settlement,[2] as in the Carlin Park project. In addition, loss of reef-associated food sources was probably substantial over this period.

No substantial habitat structure was present within at least 0.8 km of the Carlin Park reef during its burial. The closest natural structure was eastward at depths of at least 10 m. These deeper midshelf habitats may be utilized by relatively few grunt and snapper species during the newly settled and early juvenile stages. To the south, no substantial hardbottom was present for at least 4 km. To the north, the jetties of the Jupiter Inlet were approximately 2 km away. However, fishes in a northerly flight response had to negotiate a water column with zero visibility because dredge fill was dumped north-to-south. Any early stages of fish reaching the jetties would probably encounter high predation from older piscivores utilizing the large cavities among the armor-stone boulders of the artificially deepened jetty area (Lindeman, 1997a).

A postburial mitigation project using shallow artificial reefs of limestone boulders was proposed in the

[2] Hackney, C. T., M. H. Posey, and S. W. Ross. 1996. Summary and recommendations. *In* C. T. Hackney, M. H. Posey, S. W. Ross and A. R. Norris (eds.), A review and synthesis of data on surf zone fishes and invertebrates in the south Atlantic Bight and the potential impacts from beach renourishment, p. 108–111. Rep. to U. S. Army Corps of Engineers, Wilmington District, Wilmington, NC.

Carlin Park EIS. In the summer of 1998, three years after the burial, construction of approximately 1.6 ha of mitigation reefs began. If constructed before burial and at similar depths, mitigation reefs may have provided a refuge for a sizeable fraction of the thousands of displaced fishes during the burial of the hardbottom reef, as well as thousands of subsequent new recruits. Even with prompt construction of artificial reefs, many factors can limit the net production of biomass (Grossman et al., 1997). Some buried outcroppings were uncovered because of erosion of the project fill. However, structural support for two years of larval recruitment, shelter from post-settlement predation, and food for growth, were probably eliminated at the hardbottom burial site.

Nearshore hardbottom areas, such as Carlin Park, can be exposed to extended periods of wave energy and turbidity, particularly during winter months. However, conditions in winter do not dilute the potential significance of artificial burial during the spring and summer months. These are the periods of peak usage of hardbottom habitats by newly settled and juvenile stages of fishes. In the absence of dredging, nearshore areas typically show high reef exposures and reductions in physiological stressors during the spring-summer recruitment window. Elimination of this recruitment window by habitat burial for one or more years, regardless of winter dynamics, may substantially degrade the value of the primary natural nursery habitats along the windward shorelines of Florida's east coast. The above reasons suggest a risk-averse approach to hardbottom burial, as previously suggested for invertebrate fauna (Nelson, 1989).

The cumulative effects on fishes of repeated burial of nearshore habitats and other byproducts of these projects remain unknown. Cascading disturbances with ecosystem-scale effects can be hypothesized for a number of cumulative anthropogenic modifications in south Florida (e.g. Butler et al., 1995; Ault et al., 1998). Habitats affected by dredging or filling can show effects over temporal and spatial scales that are rarely considered (Vestal and Rieser, 1995; Lindeman, 1997b). For example, chronically elevated turbidities could lead to declines in primary production for frequently dredged areas of the southeast Florida shelf. Conclusive statements on the cumulative effects of large-scale dredging upon fishes will ultimately depend on the correlation of variations in early survival with adult population sizes, a rarely achieved task, even when effects may be substantial (Osenberg and Schmitt, 1996). However, the current absence of basic information on both short- and long-term scales can also be treated as an opportunity. Large dredge projects affecting midshelf and nearshore habitats will continue along the southeast Florida shelf at one- or two-year intervals. Basic questions on dredge-and-fill effects upon habitat use, predation, and growth, await study within a diverse assemblage of nearshore fishes.

Acknowledgments

J. Ault, J. Bohnsack, G. Dennis, G. Gilmore, P. Glynn, M. Harwell, and H. Wanless provided substantial review comments. Several anonymous reviewers were also very helpful. Conversations with the late David Kirtley on sabellariid reefs were consistently valuable. The assistance of these agency personnel is acknowledged: P. Davis, D. Ferrill, J. Iliff, A. Mager, and C. Sultzman. Assistance was also provided by J. Gonzalez, B. Hartig, R. Hudson, C. Leyendecker, M. Perry, R. Pugliese, M. Ridler, P. Sale, E. Schoppaul, J. Serafy, A. Stone, K. Snyder, G. Waugh, and D. Wilder. Funding was provided by the Elizabeth Ordway Dunn Foundation, the American Littoral Society, Coastal Research and Education, Inc., the South Atlantic Fishery Management Council, and the Dorr Foundation.

Literature cited

ACOE (Army Corps of Engineers).
1996. Coast of Florida erosion and storm effects study: region III with final environmental impact statement. ACOE Tech. Rep., Jacksonville District. Three volumes and appendices A-I.

Ault, J. S., J. A. Bohnsack, and G. Meester.
1998. A retrospective (1979–1996) multispecies assessment of coral reef fish stocks in the Florida Keys. Fish. Bull. 96(3):395–414.

Bray, J. R., and J. T. Curtis.
1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27:325–349.

Briggs, J. C.
1974. Marine zoogeography. McGraw-Hill, New York, NY, 475 p.

Butler IV, M. J., J. H. Hunt, W. F. Herrnkind, M. J. Childress, R. Bertelsen, W. Sharp, T. Matthews, J. M. Field, and H. G. Marshall.
1995. Cascading disturbances in Florida Bay, U.S.A.: cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobsters *Panulirus argus*. Mar. Ecol. Prog. Ser. 129:119–125.

Chiappone, M., and K. M. Sullivan.
1994. Ecological structure and dynamics of nearshore hardbottom communities in the Florida Keys. Bull. Mar. Sci. 54(3):747–756.

Culliton, T. J., M. A. Warren, T. R. Goodspeed, D. G. Remer, C. M. Blackwell, and J. J. McDonough.
1990. Fifty years of population change along the nation's coasts, 1960–2010. Second Rep. Coastal Trends Series. Strat. Assess. Branch, NOAA, 41 p.

Dennis, G. D.
1992. Resource utilization by members of a guild of benthic feeding coral reef fish. Ph.D. diss., Univ. of Puerto Rico, Mayaguez, Puerto Rico, 224 p.

Duane, D. B., and E. P. Meisburger.
1969. Geomorphology and sediments of the nearshore continental shelf, Miami to Palm Beach, Florida. USACOE Coastal Engineering Center, Tech. Memo. No. 29, 47 p.

Futch, C. R., and S. E. Dwinell.
1977. Nearshore marine ecology at Hutchinson Island, Florida: 1971–1974. IV. Lancelets and fishes. Fla. Mar. Res. Publ. No. 24, 23 p.

García-Cagide, A., R. Claro, and B. V. Koshelev.
1994. Reproducción. *In* R. Claro (ed.), Ecología de los peces marinos de Cuba, p. 187–262. Centro de Investigaciones de Quintana Roo, Mexico, 525 p.

Gauch, H. G.
1982. Multivariate analysis in community ecology. Cambridge Univ. Press, Cambridge, 298 p.

Gilmore, R. G., Jr.
1977. Fishes of the Indian River Lagoon and adjacent waters, Florida. Bull. Fl. St. Mus. Bio. Sci. 22(3), 147 p.
1992. Striped croaker, *Bairdiella sanctaeluciae*. *In* C. R. Gilbert (ed.), Rare and endangered biota of Florida. II: Fishes, p. 218–222. University Press of Florida, Gainesville, FL, 242 p.
1995. Environmental and biogeographic factors influencing ichthyofaunal diversity: Indian River Lagoon. Bull. Mar. Sci. 57(1):153–170.

Gilmore, R. G., P. A. Hastings and D. J. Herrema.
1983. Ichthyofaunal additions to the Indian River lagoon and adjacent waters, east-central Florida. Fla. Sci. 46:22–30.

Goldberg, W. M.
1973. The ecology of the coral-octocoral communities off the southeast Florida coast: geomorphology, species composition, and zonation. Bull. Mar. Sci. 23(3):465–488.

Grossman, G. D., G. P. Jones, and W. Seaman Jr.
1997. Do artificial reefs increase regional fish production? A review of existing data. Fisheries 22(4):17–23.

Hixon, M. H.
1991. Predation as a process structuring coral reef fish communities. *In* P. F. Sale (ed.), The ecology of fishes on coral reefs, p. 475–500. Academic Press, San Diego, CA, 754 p.

Hoffmeister, J. E.
1974. Land from the sea: the geologic story of south Florida. Univ. Miami Press, Coral Gables, FL, 143 p.

Humann, P.
1994. Reef fish identification: Florida, Caribbean, Bahamas. New World Press, Jacksonville, FL, 396 p.

Jongman, R. H. G., C. J. F. ter Braak, and O. F. R. van Tongeren (eds).
1995. Data analysis in community and landscape ecology. Cambridge Univ. Press, Cambridge, 299 p.

Jones, G. P.
1991. Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. *In* P. F. Sale (ed.), The ecology of fishes on coral reefs, p. 294–330. Academic Press, San Diego, CA, 754 p.

Kirtley, D. W.
1994. A review and taxonomic revision of the family Sabellariidae, Johnston, 1865 (Annelida; Polychaeta). Sabecon Press Science Series 1, Vero Bch., FL, 223 p.

Kirtley, D. W. and W. F. Tanner.
1968. Sabellariid worms: builders of a major reef type. J. Sed. Petrol. 38(1):73–78.

Lindeman, K. C.
1986. Development of larvae of the French grunt, *Haemulon flavolineatum*, and comparative development of twelve western Atlantic species of *Haemulon* (Percoidei, Haemulidae). Bull. Mar. Sci. 39(3):673–716.
1997a. Development of grunts and snappers of southeast Florida: cross-shelf distributions and effects of beach management alternatives. Ph.D. diss., Univ. Miami, Coral Gables, FL, 419 p.
1997b. Comparative management of beach systems of Florida and the Antilles: applications using ecological assessment and decision support procedures. *In* G. Cambers (ed.), Managing beach resources in the smaller Caribbean islands, p. 134–164. UNESCO Coastal Region and Small Island Paper 1, 269 p.

Lindeman, K. C., G. A. Diaz, J. E. Serafy, and J. S. Ault.
1998. A spatial framework for assessing cross-shelf habitat use among newly-settled grunts and snappers. Proc. Gulf Carib. Fish. Inst. 50:385–416.

NRC (National Research Council).
1995. Beach nourishment and protection. National Academy Press, Washington, DC, 334 p.

Nelson, W. G.
1989. Beach nourishment and hard bottom habitats: the case for caution. *In* S. Tait (ed.), Proc. 1989 National Conf. Beach Preserv. Technol., p. 109–116. Fl. Shore and Beach Preserv. Assoc., Tallahassee, FL.

Nelson, W. G., and L. Demetriades.
1992. Peracariids associated with sabellariid worm rock (*Phragmatopoma lapidosa* Kinberg) at Sebastian Inlet, Florida, U.S.A. J. Crust. Biol. 12(4):647–654.

NOAA (National Oceanic and Atmospheric Administration).
1996. Magnusen-Stevens Fishery Conservation and Management Act, as amended through Oct. 11, 1996. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-F/SPO-23, 121 p.

Osenberg, C. W., and R. J. Schmitt.
1996. Detecting ecological impacts caused by human activities. *In* R. J. Schmitt and C. W. Osenberg (eds.), Detecting ecological impacts, p. 3–15. Academic Press, San Diego, CA, 401 p.

Palm Beach County Dept. Environ. Resources Management.
1994. Palm Beach County, Florida, shore protection project, from Martin County line to Lake Worth Inlet and from south Lake Worth Inlet to Broward County line: Jupiter/Carlin segment. Final supplemental environmental impact statement. Submitted to USACOE, Jacksonville District Office, 80 p. with appendices.

Richards, W. J., and K. C. Lindeman.
1987. Recruitment dynamics of reef fishes; planktonic processes, settlement and demersal ecologies, and fishery analysis. Bull. Mar. Sci. 41(2):392–410.

Robins, C. R., and G. C. Ray.
1986. A field guide to Atlantic coast fishes of North America. Houghton Mifflin Co., Boston, MA, 354 p.

Rohlf, F. J.
1997. NTSYS-pc: numerical taxonomy and multivariate analysis system, version 2.0. Exeter Publishing, Setauket, NY, 31 p.

Ross, S. T., R. H. McMichael Jr., and D. L. Ruple.
1987. Seasonal and diel variation in the standing crop of fishes and macroinvertebrates from a Gulf of Mexico surf zone. Estuarine Coastal Shelf Sci. 25:391–412.

Ruple, D. L.
1984. Occurrence of larval fishes in the surf zone of a northern Gulf of Mexico barrier island. Estuarine Coastal Shelf Sci. 18:191–208.

Sale, P. F.
1980. The ecology of fishes on coral reefs. Oceanogr. Mar. Biol. 18:367–421.
Sedberry, G. R., and R. F. Van Dolah.
1984. Demersal fish assemblages associated with hard-bottom habitat in the South Atlantic Bight of the U. S. A. Environ. Biol. Fishes 11(4):241–258.
Serafy, J. E., K. C. Lindeman, T. E. Hopkins, and J. S. Ault.
1997. Effects of freshwater canal discharges on subtropical marine fish assemblages: field and laboratory observations. Mar. Ecol. Prog. Ser. 160:161–172.
Shulman, M. J., and J. C. Ogden.
1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish, *Haemulon flavolineatum*. Mar. Ecol. Prog. Ser. 39:233–242.
Sneath, P. H. A., and R. R. Sokal.
1973. Numerical taxonomy, the principles and practice of numerical classification. W.H. Freeman and Co., San Francisco, CA, 573 p.
Starck, W. A.
1970. Biology of the gray snapper, *Lutjanus griseus* (Linnaeus), in the Florida Keys. Stud. Trop. Oceanogr. Univ. Miami 10:11–150.
Stewart-Oaten, A.
1996. Goals in environmental monitoring. *In* R. J. Schmitt and C. W. Osenberg (eds.), Detecting ecological impacts, p. 17–26. Academic Press, San Diego, CA, 401 p.
Stewart-Oaten, A., W. W. Murdoch, and K. R. Parker.
1986. Environmental impact assessment: "pseudoreplication" in time? Ecology 67:929– 940.
ter Braak, C. J. F.
1988. CANOCO—a FORTRAN program for canonical community ordination. Microcomputer Power, Ithaca, NY, 95 p.
Vare, C. N.
1991. A survey, analysis, and evaluation of the nearshore reefs situated off Palm Beach County, Florida. M.S. thesis, Florida Atlantic Univ., Boca Raton, FL, 165 p.
Vestal, B. and A. Rieser.
1995. Part I - Syntheses, with annotated bibliography. In: Methodologies and mechanisms for management of cumulative coastal environmental impacts. NOAA Coastal Ocean Program Decision Analysis Series No. 6. NOAA Coastal Ocean Office, Silver Springs, MD, 139 p.

Appendix

Total abundances of all species visually surveyed at three nearshore hardbottom sites, southeast Florida. Only predredging data were used for Carlin Park site. * = hypothesized to use nearshore hardbottom as a nursery habitat (see discussion).

Rank	Common name	Species	Coral Cove	Carlin Park	Ocean Ridge	Total
1	Sailors choice	*Haemulon parra**	649	555	122	1326
2	Silver porgy	*Diplodus argenteus**	344	647	132	1123
3	Cocoa damselfish	*Stegastes variabilis**	420	600	66	1086
4	Slippery dick	*Halichoeres bivittatus**	439	327	50	816
5	Hairy blenny	*Labrisomus nuchipinnis**	463	262	81	806
6	Sergeant major	*Abudefduf saxatilis**	367	199	112	678
7	Black margate	*Anisotremus surinamensis**	513	68	55	636
8	Porkfish	*Anisotremus virginicus**	331	174	61	566
9	Tomtate	*Haemulon aurolineatum**	245	295	8	548
10	Grunt sp.	*Haemulon* sp.*	266	233	34	533
11	French grunt	*Haemulon flavolineatum**	134	210	43	387
12	Smallmouth grunt	*Haemulon chrysargyreum**	60	222	10	292
13	White grunt	*Haemulon plumieri**	70	150	1	221
14	Glassy sweeper	*Pempheris schomburgki**	153	21	32	206
15	Dusky damselfish	*Stegastes fuscus**	75	83	9	167
16	High-hat	*Equetus acuminatus**	54	59	13	126
17	Ocean surgeon	*Acanthurus bahianus**	51	12	17	80
18	Doctorfish	*Acanthurus chirurgus**	63	2	7	72
19	Redfin parrotfish	*Sparisoma rubripinne**	52	14	2	68
20	Mojarra sp.	*Eucinostomus* sp.	37	20	2	59
21	Spanish grunt	*Haemulon macrostomum**	14	35	1	50
21	Yellow jack	*Caranx bartholomaei*	9	41	0	50
23	Yellow goatfish	*Mulloidichthys martinicus*	34	8	0	42
24	Lane snapper	*Lutjanus synagris**	23	12	3	38
25	Bluehead wrasse	*Thalassoma bifasciatum*	22	7	7	36
25	Croaker sp.	Sciaenid sp.	22	14	0	36
27	Redtail parrotfish	*Sparisoma chrysopterum**	16	14	3	33
28	Damselfish sp.	*Stegastes* sp.	9	5	18	32
29	Parrotfish sp.	*Sparisoma* sp.	14	14	0	28
30	Reef croaker	*Odontoscion dentex**	13	3	8	24
30	Bar jack	*Caranx ruber*	2	20	2	24
32	Chub sp.	*Kyphosus* sp.	10	4	9	23
33	Bridled goby	*Coryphopterus glaucofraenum*	2	19	1	22
34	Clown wrasse	*Halichoeres maculipinna**	8	5	4	17
35	Anchovy sp.	Engraulid sp.	15	0	0	15
36	Puddingwife	*Halichoeres radiatus**	4	6	4	14
36	Orangespotted filefish	*Cantherhines pullus*	2	11	1	14
38	French angelfish	*Pomacanthus paru**	5	5	3	13
39	Seaweed blenny	*Parablennius marmoreus*	2	5	5	12
40	Caesar grunt	*Haemulon carbonarium**	3	7	1	11
41	Yellowtail snapper	*Ocyurus chrysurus**	3	5	2	10
41	Striped croaker	*Bairdiella sanctaeluciae**	10	0	0	10
43	Stoplight parrotfish	*Sparisoma viride*	4	1	4	9

continued

Appendix (continued)

Rank	Common name	Species	Coral Cove	Carlin Park	Ocean Ridge	Total
43	Redband parrotfish	*Sparisoma aurofrenatum*	1	0	8	9
44	Gray snapper	*Lutjanus griseus*	6	0	2	8
44	Porgy sp.	Sparid sp.	0	8	0	8
44	Bluestriped grunt	*Haemulon sciurus*	2	4	2	8
44	Spanish sardine	*Sardinella aurita*	8	0	0	8
49	Molly miller	*Scartella cristata**	2	5	0	7
49	Blackear wrasse	*Halichoeres poeyi*	6	1	0	7
51	Sheepshead	*Archosargus probatocephalus*	1	5	0	6
51	Blue tang	*Acanthurus coeruleus**	3	3	0	6
51	Spotted goatfish	*Pseudupeneus maculatus*	3	0	3	6
54	Saddled blenny	*Malacoctenus triangulatus**	1	3	1	5
55	Barbfish	*Scorpaena plumieri*	2	2	0	4
55	Queen parrotfish	*Scarus vetula*	0	1	3	4
57	Flamefish	*Apogon maculatus*	0	3	0	3
57	Yellowfin mojarra	*Gerres cinereus*	3	0	0	3
57	Blue runner	*Caranx crysos*	3	0	0	3
57	Spotfin butterflyfish	*Chaetodon ocellatus*	0	1	2	3
61	Balloonfish	*Diodon hystrix*	1	0	1	2
61	Chain moray	*Echidna catenata*	2	0	0	2
61	Scrawled cowfish	*Lactophrys quadricornis*	1	0	1	2
61	Schoolmaster	*Lutjanus apodus*	2	0	0	2
61	Blenny sp.	Bleniid sp.	2	0	0	2
61	Cottonwick	*Haemulon melanurum*	2	0	0	2
61	Great barracuda	*Sphyraena barracuda*	1	0	1	2
61	Scrawled filefish	*Aluterus scriptus*	1	0	1	2
69	Bicolor damselfish	*Stegastes partitus*	0	0	1	1
69	Orangespotted goby	*Nes longus*	0	1	0	1
69	Spanish hogfish	*Bodianus rufus*	0	1	0	1
69	Spotted snake eel	*Myrichthys acuminatus*	0	1	0	1
69	Gray angelfish	*Pomacanthus arcuatus**	1	0	0	1
69	Sharpnose puffer	*Canthigaster rostrata*	1	0	0	1
69	Greater soapfish	*Rypticus saponaceus*	1	0	0	1
69	Smooth trunkfish	*Lactophrys triqueter*	1	0	0	1
69	Hogfish	*Lachnolaimus maximus*	0	1	0	1
69	Puffcheck blenny	*Labrisomus bucciferus*	1	0	0	1
69	Nurse shark	*Ginglymostoma cirratum*	0	1	0	1
69	Squirrelfish	*Holocentrus rufus*	0	1	0	1
69	Blue angelfish	*Holacanthus bermudensis**	0	0	1	1
69	Rosy blenny	*Malacoctenus macropus*	0	1	0	1
69	Spotted moray	*Gymnothorax moringa*	1	0	0	1
69	Goldentail moray	*Muraena miliaris*	0	1	0	1
69	Atlantic spadefish	*Chaetodipterus faber*	1	0	0	1
69	Sand drum	*Umbrina coroides*	1	0	0	1
		Total taxa	72	60	50	86
		Total individuals	5093	4438	960	10491

Growth and maturation of the ghost shrimp *Lepidophthalmus sinuensis* Lemaitre and Rodrigues, 1991 (Crustacea, Decapoda, Callianassidae), a burrowing pest in penaeid shrimp culture ponds*

Sergio F. Nates

Darryl L. Felder

Department of Biology and Laboratory for Crustacean Research,
University of Southwestern Louisiana
Lafayette, Louisiana 70504-2451

E-mail address (for D. L. Felder, contact author): dlf4517@usl.edu

Abstract.—Growth and sexual maturation were studied in the ghost shrimp *Lepidophthalmus sinuensis*, a pest species infesting oligohaline penaeid shrimp culture ponds on the Caribbean coast of Colombia. Sex ratio was significantly female-biased over four years of sampling. Development of ovaries, indexed as relative width, peaked prior to peak occurrence of ovigerous females and either coincided with or immediately followed the quarter of lowest ambient salinity. Ovigerous females occurred in all months, but the greatest mean percentage occurred in the first or second quarter of each year. Size and coloration of ovaries varied by maturational stage, and monthly counts of eggs per female peaked in February–April. Detection of recruits <8–10 mm carapace length (CL) was sporadic, and tracking of growth in recruitment cohorts was not possible. Mean CL of the population increased slowly over the first two years of sampling, as the percentage of males in the population increased. Sexual maturity in both males and females was evident in relative growth changes of the major chela. Analysis of growth in chela width, scaled to carapace length, suggested that males mature at about 11.0–11.3 mm CL, whereas females mature near 10.8–11.2 mm CL. Prematuration positive allometric growth did not differ between sexes, whereas postmaturation negative allometric growth in females differed significantly from strongly positive allometric growth in postmaturation males. Relative growth in wet weight of postmaturation males significantly exceeded that of postmaturation females. Expected female weight accumulations from episodic ovarian development were perhaps offset by simultaneous negative postmaturation growth of the female major chela. An understanding of growth, maturation, and the reproductive cycle of this shrimp species will help develop management strategies to control infestations by this callianassid pest species.

Manuscript accepted 14 August 1998.
Fish. Bull. 97:526–541 (1999).

In northern South America, the ghost shrimp *Lepidophthalmus sinuensis* Lemaitre and Rodrigues has been found restricted to oligohaline estuaries on the Caribbean coast of Colombia (Lemaitre and Rodrigues, 1991). From previous study of a congeneric species, osmoregulatory capacity and tolerance of hypoxia in this genus (Felder, 1978, 1979; Felder et al., 1986) appear to exceed abilities reported in most other callianassid genera (Thompson and Pritchard, 1969; Forbes, 1974, 1978; Mukai and Koike, 1984; Posey, 1987). Such adaptation has allowed members of the genus to exploit extensively low salinity habitats, especially richly organic silty bars and banks of lower river mouths or intertidal mudflats (Felder and Manning, 1997). In *L. sinuensis* and some eastern Pacific congeners (Nates and Felder, 1998), this adaptation also includes sediments of tropical, estuarine ponds in which penaeid shrimp are cultured.

Dense accumulations of ghost shrimp in these penaeid culture ponds are favored by their abbreviated larval development (Nates et al., 1997). At high levels of infestation by these burrowers, metabolic impacts and bioturbation appear to decrease penaeid shrimp production by reducing survival rates of postlarvae and slowing growth to marketable size (Nates and Felder, 1998). A thorough understanding of maturation and reproductive cycles in *L. sinuensis* is essential to devising effective long-term control measures for such infestations, especially to limit or replace the pesticide treatments that have been used to date (Nates and Felder, 1998). Thus far, timing and frequency of pesticide applications in shrimp mariculture have been devised by trial and error effects on penaeid production, without specific attempts to target treatments to peaks in reproductive activity of ghost shrimp or to achieve control by modifications in water management.

Although some species of the Callianassidae burrow to depths of 2 m or more (Pohl, 1946; Poore and Suchanek, 1988; Manning and Felder, 1991; Felder and Griffis, 1994), the difficulty of monitoring many natural populations has been overcome by collecting them with yabby pumps (see Manning, 1975). Several aspects of population biology for varied genera are now well documented (Pohl, 1946; Hailstone and Stephenson, 1961; Phillips,

* Contribution 57 from the University of Southwestern Louisiana, Laboratory of Crustacean Research, Lafayette, LA 70504-2451.

1971; Poore and Suchanek, 1988; Witbaard and Duineveld, 1989; Tamaki and Ingole, 1993; Rowden and Jones, 1994, 1995; Dumbauld et al., 1996), and the importance of callianassids in sediment turnover and nutrient cycling has been noted (Rowden and Jones, 1993; Ziebis et al., 1996). Ecological impacts of *Lepidophthalmus* spp. can dominate those of other estuarine infauna, as noted in recent studies of the warm-temperate species *L. louisianensis* in the northern Gulf of Mexico (Felder and Lovett, 1989; Felder and Griffis, 1994) and the tropical species *L. sinuensis* on the Caribbean coast of Colombia (Nates and Felder, 1998). Larval life histories for both *L. louisianensis* and *L. sinuensis* have been described (Nates et al., 1997), but later life stages and maturation remain little known for the tropical species *L. sinuensis*. Objectives of the present study were to analyze the periodicity and frequency of reproductive activity, to determine rates of growth in morphological features, and to define allometric indicators of maturation for populations of *L. sinuensis*. Resulting implications for management of penaeid shrimp ponds are discussed.

Materials and methods

All animals were obtained at the Agrosoledad S.A. shrimp farm on the upper Cispata estuary of the Río Sinú, Departamento de Cordoba, Colombia, near 9°17'N, 75°50'W. In order to avoid overt effects of pond harvesting, feeding, and other management activity, collections were restricted to bottom sediments of earthen drainage canals that extend for several kilometers through the farm. Specimens were individually extracted from burrows with yabby pumps (Manning, 1975), and samples included all animals retained when extracted sediments were washed on coarse (5-mm) sieves. All population samples were taken within 500 m of the upper end (origin) of the drainage canal system where colonized bottom muds ranged from about 3 to 6 m in width and population density ranged from 15 to 40 animals per m^2.

Monthly sampling of populations extended over four years from December 1991 through December 1995. Each monthly sample consisted of animals obtained from burrow openings encountered at random during walks along transects that crossed exposed mudflats at the sampling site during a period of reduced pond discharge. The sample consisted of at least 60 animals, and over 3200 animals were collected in the course of the study. Following collection, animals were transported in individual perforated vials (Felder, 1978) to the farm laboratory for morphological analysis. Specimens lacking chelipeds, having incompletely regenerated chelae, or with other obvious appendage deformities were excluded from the analyses that involved measures of those appendages but included in analyses of population size-class structure. In the laboratory, each individual was sexed on the basis of anterior pleopod morphological features and evidence of ovaries visible through the integument. Wet weight (WW) was determined to ±0.1 g on a top-loading balance after animals were blotted with tissue paper. Dry weight was estimated by drying the animals at 60°C for 48 h, and ash content was estimated from weight after ignition at 500°C for 6 h. When present, eggs on pleopods were included in weights of ovigerous females.

Morphometric measurements (Felder and Lovett, 1989) were made with dial calipers to ±0.05 mm. Because carapace length (CL) is usually less dependent on gonadal development than are most other size measurements (Hartnoll, 1982; Felder and Lovett, 1989), it was selected to represent body size and measured from the tip of the rostrum to the posterior margin of the cardiac region. Total length (TL) was measured from the tip of the rostrum to the posterior margin of the extended telson. Major chela height (ChH) was measured as the maximum height of the propodus, inferior margin to superior margin. Major chela width (ChW) was measured as the maximum width of the propodus from the most convex area on the internal surface to the opposite convex area on the external surface. Major chela length (ChL) was measured as the maximum length from the superior proximal articulation of the propodus with the carpus to the superior distal articulation with the dactylus. Between November 1992 and December 1995, ovarian width (OW) of females (the width of the right ovary visible dorsally through the integument of the third abdominal segment) was determined. An index of relative ovarian development was estimated from the ratio OW/CL. Color and number of eggs, color of the ovaries, evidence of parasites, and occurrence of damaged or missing chelae were also recorded. Egg size was measured under a light microscope and ocular micrometer. Volume of the eggs was calculated from the mean of the long and short axes used as the single diameter measurement for a sphere (McEdward and Chia, 1991).

Temperature and salinity were measured twice daily (dawn and dusk) at the surface and bottom of filled ponds. Temperature was measured ±1 °C with the probe of a YSI® model 57 temperature-compensated oxygen meter. Salinity ±1 ppt was measured with a temperature-compensated refractometer.

All means were reported along with the 95% CI (confidence interval). Monthly population samples were pooled to compare quarterly variations in the

distribution of size cohorts and the occurrence of ovigerous females in the population. Temporal trends in both carapace lengths and sex ratios for the overall four-year span of the study were analyzed by linear-linear piecewise polynomial regression to define slope transition points. Percentile data for the sex ratios were arcsine-transformed prior to these analyses. In order to remove effects of morphologically anomalous postreproductive and senescent individuals, animals >18.0mm CL (two females and three males) were excluded from analyses of relative growth. Linear-linear piecewise polynomial analysis of untransformed data was used to optimize positioning of ontogenetic transition points (±0.05 mm) in all relative growth comparisons. Except for this alternative method of iteratively locating slope transitions, methods complied with the recommended practice of fitting regressions to untransformed data above and below transition points by reduced major axis (Lovett and Felder, 1989). Standard allometric coefficients (Huxley, 1932) were also determined from regressions of log-transformed data by least squares estimate, with data subdivided at the previously estimated transition points. All statistical analyses were performed with NCSS® (Number Cruncher Statistical System) 6.0 software (Hintz, 1995).

Because generic revisions have yet to address many of the confamilial taxa that are treated in our comparative discussions, it was necessary in comparative discussions to refer to some species under *Callianassa sensu lato* (s.l.), while acknowledging that *Callianassa sensu stricto* has been restricted to a few eastern Atlantic populations (see Manning and Felder, 1991).

Results

Sex ratio

Except for January to June 1992, March 1993, and February 1995, sex ratios were significantly female-biased over the four years of sampling (Fig. 1A). Over the entire study period, the mean sex ratio was 2.4 ±0.3 females per male, with the lowest mean ratio (1.1) occurring in February 1992, and the highest ratio (5.1) in October 1993. Trends in mean CL of the population (Fig. 1B) generally tracked those in sex ratios, as defined by piecewise regression analysis. Slopes over the first two years revealed declining relative abundance and increasing mean CL of males, patterns that differed significantly from those of the last two years of monitoring. An iteratively optimized transition point for sex ratios occurred at 23 months, whereafter mean sex ratios remained near asymptotic. Analysis over the full study period also defined an optimized transition point or peak in CL of males at 23 months, beyond which male CL was asymptotic. The CL of females, however, peaked late in the first year of monitoring.

Mean size of both males and females increased slightly but significantly from the first through fourth quarter of each year except for 1994, a year in which the presence of first quarter recruits was offset by a cohort of large individuals surviving from the previous year (Fig. 2). When treated separately, mature-sized individuals (>11 mm CL) of both male and female populations increased in mean CL over the year, usually peaking in the fourth quarter prior to maximum abundance of ovigerous females in the following year (Fig. 3, B and D). Mean CL of males appeared to exceed slightly that of females over the full study period, and males dominated large size classes (Figs. 1B, 2, 3B). Only 4.3% of the collected females were >15.0 mm CL, whereas 12.4% of males attained this size. The largest animal collected was a 20.7-mm-CL male. Detection of recruits <8–10 mm CL was sporadic throughout the study (Fig. 3E), and tracking of growth in recruitment cohorts was not possible.

Ovigerous females

Among all ovigerous females collected during the study (n=444), size ranged from 7.04 mm CL to 16.8 mm CL. However, 38.3% of all these were in the 13.0 to 13.9 mm CL size class and <1.5% of ovigerous females were <11.0 mm CL (Fig. 4). The single ovigerous specimen <9.8 mm CL was an apparently precocious individual taken in August 1994, while the population of ovigerous females was low (Fig. 3D). During peak abundances of ovigerous females (February to June, Fig. 5B), 64.3% of females in the 13.0 to 13.9 mm CL size class were ovigerous (Fig. 2).

Ovigerous females were found in all months of the four-year study (Figs. 2 and 3D). However, percentages were lowest in the third quarters of 1992, 1993, and 1995, and the fourth quarter of 1994, whereas the highest percentages occurred in the first or second quarter of each year. Peak abundance of ovigerous females coincided with the highest quarterly salinity in 1992, 1994, and 1995 but was less defined in 1993 when the fourth quarter salinity did not fall to a typical low value (Fig. 3, A and D). When monthly samples were pooled over the entire study, highest percentages of ovigerous individuals among all females were evident during the high salinity period from February to June; a maximum was found in May (35.7%), three months after peak development of the ovaries (Fig. 5, A–C).

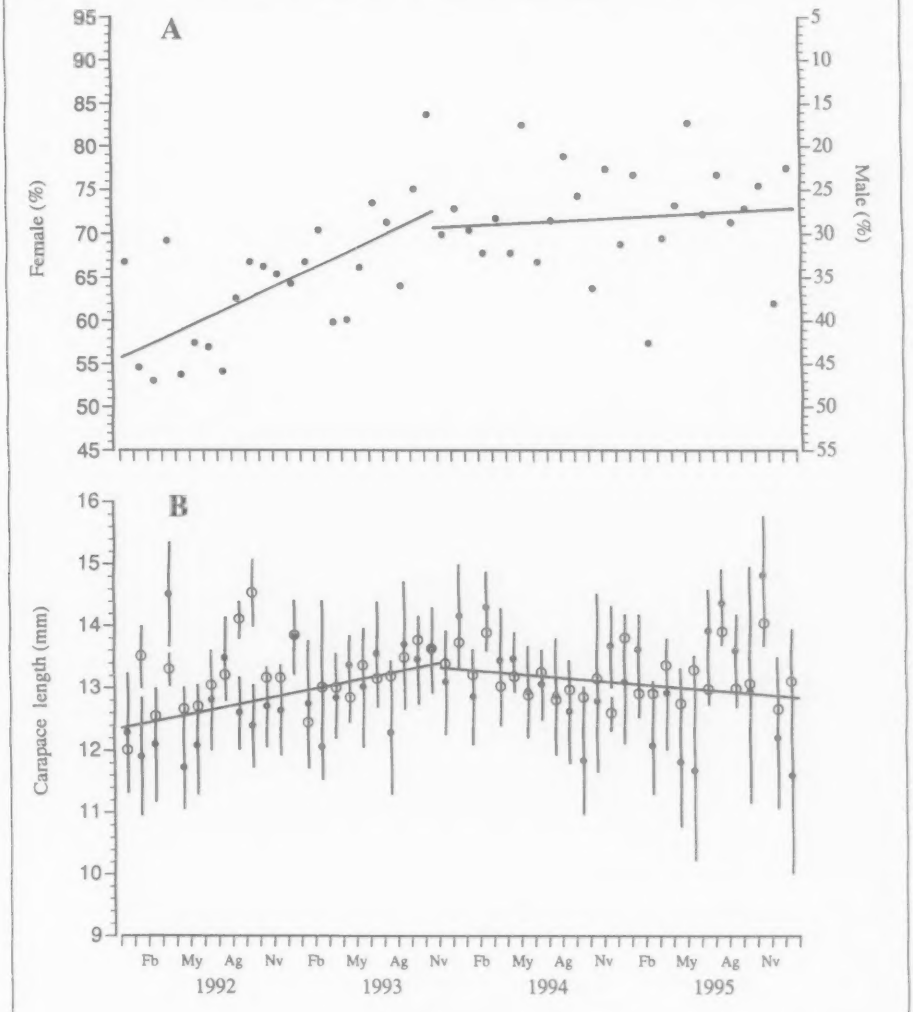


Figure 1

Sex composition (**A**) and mean carapace length (CL) (**B**) in sampled Colombian populations of *Lepidophthalmus sinuensis*, December 1991 through December 1995. Mean CL is shown separately for males (closed circles) and females (open circles); vertical lines define 95% CI. The transition point at which data are subdivided, estimated by piecewise linear-linear polynomial regression, was selected to minimize the sum of squares of residuals.

Development of ovaries reached maxima in the quarter prior to peak occurrences of ovigerous females and either coincided with or immediately followed the quarter in which lowest ambient salinities occurred (Fig. 3, A, C, and D). Examined as a monthly value pooled over the three years that it was monitored (Fig. 5C), this index of ovarian development was at minimum values in June and July when ovaries of many spent and immature females, although evident for the full length of the abdomen, were limited in width to narrow translucent-yellow strands. Ovaries became deep yellow to yellow-orange as relative ovarian width began to increase markedly in August, concurrent with an annual decline in ambient salinity. By October, ovaries of most mature females were somewhat lobate in shape and yellow-orange to reddish orange in color, and ovarian index reached high values that persisted through

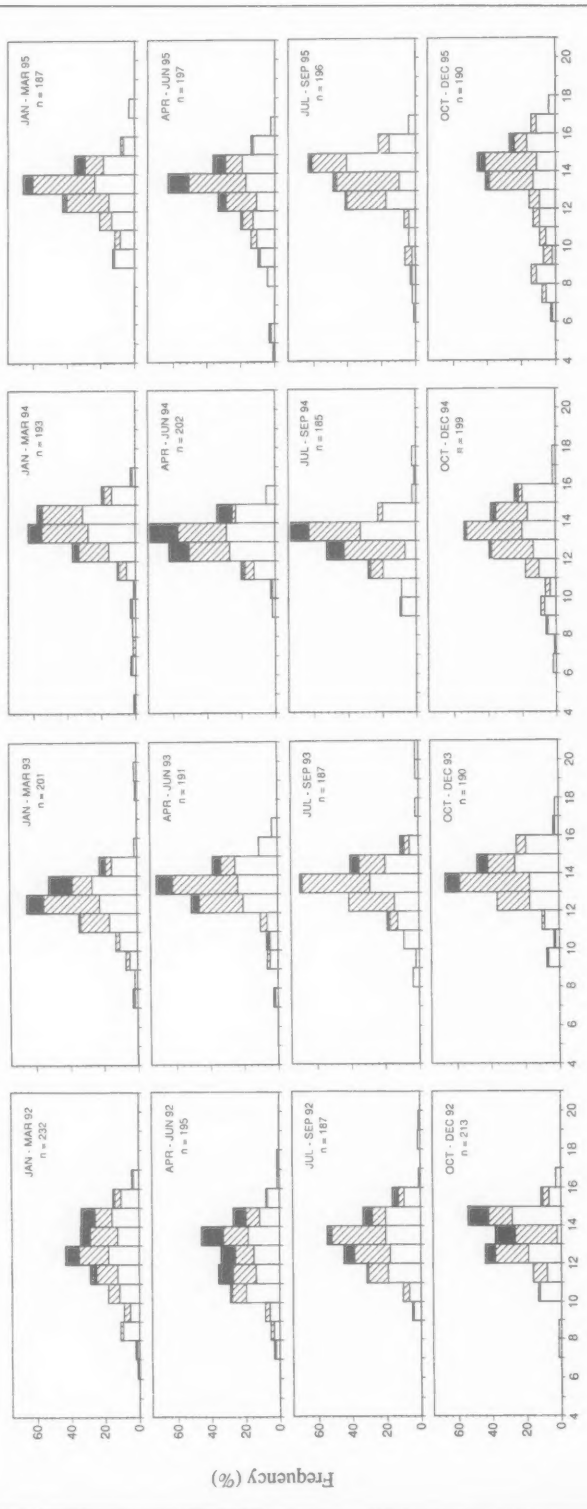

JAN - MAR 95 n = 187
APR - JUN 95 n = 197
JUL - SEP 95 n = 196
OCT - DEC 95 n = 190
JAN - MAR 94 n = 193
APR - JUN 94 n = 202
JUL - SEP 94 n = 185
OCT - DEC 94 n = 199
JAN - MAR 93 n = 201
APR - JUN 93 n = 191
JUL - SEP 93 n = 187
OCT - DEC 93 n = 190
JAN - MAR 92 n = 232
APR - JUN 92 n = 195
JUL - SEP 92 n = 187
OCT - DEC 92 n = 213
Frequency (%)
Carapace length (mm)

Figure 2

Quarterly size class (CL) frequency distributions for males (open bars), nonovigerous females (hatched bars), and ovigerous females (solid bars) in sampled Colombian populations of *Lepidophthalmus sinuensis*, January 1992 through December 1995 (*n*=sample size).

February. Highest values for the ovarian index, in February (0.139 ±0.012), were significantly greater than were preceding values in December or those that followed in March through May. Decreasing measures of relative ovarian width during April through June (Figs. 3C and 5C) were coincident with the second quarter maxima in abundance of ovigerous females (Fig. 3D and 5B) because many of those females had spent ovaries.

Shape of the eggs was almost spherical in recently deposited pale yellow to yellow-orange clutches and became more oblong as color faded to translucent gray-brown in late-stage eggs just prior to hatching. Mean egg volume in live late stage eggs was 0.81 ±0.07 mm^3 (n=76 eggs, from 5 different females), and the coefficient of variation in volume within a single egg clutch was 5.09% (n=30); mean dimensions were 1.22 ±0.04 mm by 1.05 ±0.02 mm. The total number of eggs per female ranged from 182 ±44 in small females (<12.0 mm CL; n=30) to 301 ±36 in large females (≤14.0 mm CL; n=141). The overall mean number of eggs for all ovigerous females collected was 251 ±18 (n=444), and the maximum number found on any single female was 958 on a specimen of 14.2 mm CL. Monthly egg counts per ovigerous female, pooled over the study (Fig. 5D), revealed peak abundances in February–April, followed by significantly lower numbers in June–July. Thus, the overall rate of egg production, when considered as a product of both abundance of ovigerous females and egg

abundance per clutch (Fig. 5, B and D), was maintained at particularly elevated levels from February through at least April and perhaps May.

Growth and sexual maturation

Size at sexual maturation in both males and females of the sampled population was evident in relative growth changes of the major chela. Asymmetry of the first pereopodal chelae was clearly evident in both sexes and did not show bias for right or left handedness in random subsamples (left:right handedness 23:27 for males, 25:25 for females; n=50 per sex). The value of this feature as a secondary sex character was suggested initially by the much heavier general appearance of the appendage in large males than in females of approximately the same size, and sexual differences in allometric growth were documented subsequently by regression analyses of morphological measurements (Fig. 6; Tables 1 and 2).

Relative growth rate in the chela width of males increased in animals that had reached a mean carapace length of at least 11.3 mm, as estimated by linear-linear piecewise polynomial regression analysis (Fig. 6A). Independent regression analysis of males larger and smaller than this size by reduced major axis revealed significant differences in slopes for those data sets (Table 1), even though the two values for this positive allometric growth did not differ significantly when compared as allometric coefficients (Table 2). When fitted by reduced major axis, regression slopes for both premature and postmaturation phases of growth in female chela width (Fig. 6B) differed significantly from those for both growth phases in males, although there was far greater difference between the sexes in the postmaturation phase. Relative growth in the chela width of females became significantly less positive beyond a carapace length near 10.8 mm. The negative allometric growth (coefficient <1) for this postmaturation phase in females (Table 2) differed significantly from the strongly positive allometric growth in postmaturation males.

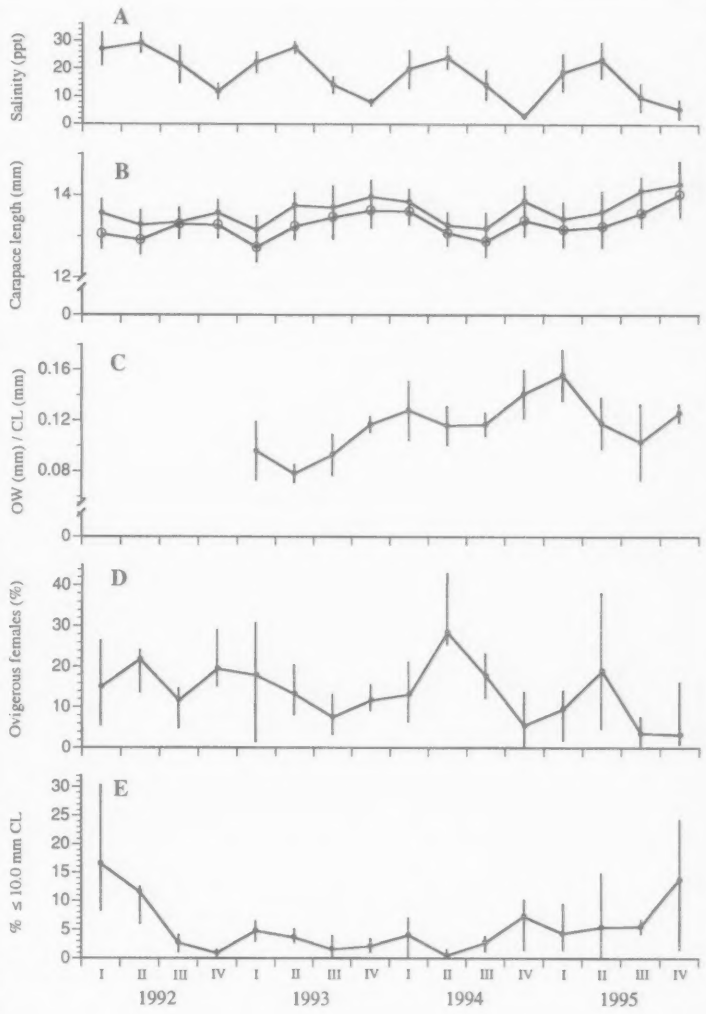


Figure 3

Quarterly measures of salinity, growth, and reproductive indices in sampled Colombian populations of *Lepidophthalmus sinuensis*, January 1992 through December 1995; for A–C, vertical lines define 95% CI; for D–E, vertical lines define range. (**A**) Morning surface salinity (ppt) at the farm intake pump station in the upper estuary, expressed as mean of daily measures throughout each quarter; (**B**) mean CL of mature (>11 mm CL) males (closed circles) and females (open circles) in sampled populations; (**C**) relative ovarian development (OW/CL); (**D**) percentage of ovigerous individuals among females; (**E**) percentage of juveniles (≤10.00 mm CL).

Analysis of relative growth in major chela height for males (Fig. 6C) and females (Fig. 6D), when scaled to carapace length, produced remarkably similar results to that for relative growth in chela width, suggesting some interdependency of those measures. Transition points were optimally located at a mean carapace length of 11.0 mm for males and 11.2 mm for females, and postmaturation growth differed significantly between the sexes (Table 1). On the basis of allometric coefficients (Table 2), positive prematuration allometric growth once again did not differ between the sexes, whereas negative postmaturation growth in females differed significantly from the strongly positive allometric growth in postmaturation males. Analysis of chela width scaled to chela height in both sexes did not indicate significant prematuration differences between males and females, and growth in both sexes was isometric or nearly so (Tables 1 and 2). However, following transition to the postmaturation phase in males, relative growth in chela width exceeded that of height. The opposite effect was seen in postmaturation females; negative allometric growth was seen in chela width, when compared to chela height.

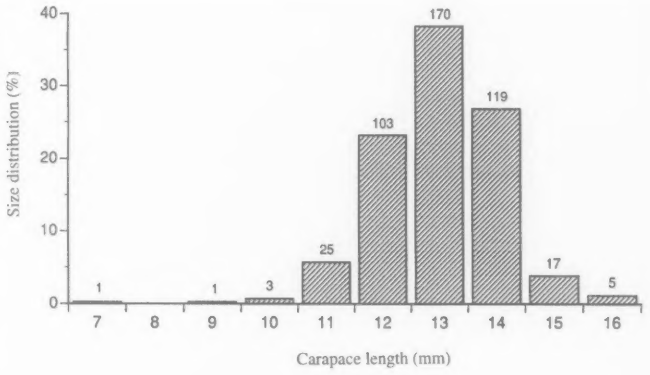


Figure 4

Size class (CL) frequency distribution of all ovigerous females in sampled Colombian populations of *Lepidophthalmus sinuensis*, December 1991 through December 1995 (number by class appears above each bar).

Analysis of total length scaled to carapace length revealed large measures of error (Tables 1 and 2), as expected in size measurements that include the length of a soft, stretchable abdomen. Allometric coefficients indicated that slopes did not significantly differentiate prematuration growth from an isometric pattern in either sex, whereas postmaturation growth on the basis of this parameter appeared to be negatively allometric but similar in rate for both males and females.

Large measures of error associated with wet weight measurements in relation to carapace length, especially at small sizes, limited detection of possible sex differences in allometric coefficients based upon this parameter and did not resolve significant differences between growth phases of either sex (Table 2). Only in the postmaturation phase were allometric coefficients based upon wet weight significantly more positive in males than in females. The more sensitive analyses of wet weight based upon regressions by reduced major axis (Fig. 7, A and B; Table 1) detected highly significant differences between postmaturation males and females, regardless of whether ovigerous females were included or excluded from the analysis, and also resolved significant differences in rates of mass accumulation between prematuration and postmaturation growth phases. Optimized transition points in piecewise regression analyses of wet weight to length relationships were near 9.8 mm CL for females and near 11.3 mm CL for males. These regression breaks suggest that maturation in males occurs at slightly higher wet weights (1.5 to 2 g) than in females (usually near 1 g).

Dry weights and ash free dry weights were determined for limited subsets of our sample and were not subjected to regression analysis. The proportional relation of dry to wet weight in ovigerous females (0.47 ± 0.06; $n=8$) was slightly but significantly higher than in nonovigerous females (0.36 ± 0.03; $n=76$) and males (0.33 ± 0.05; $n=12$), whereas the relation of ash free dry weight to wet weight in ovigerous females (0.052 ± 0.003; $n=8$) was not significantly different from that of either nonovigerous females (0.059 ± 0.011; $n=41$) or males (0.055 ± 0.003; $n=2$).

Discussion

Sex ratio

Strongly female-biased sex ratios in the monitored population of *Lepidophthalmus sinuensis* are in marked contrast to those reported in intertidal populations of *L. louisianensis* on the Mississippi coast in the northern Gulf of Mexico (Felder and Griffis, 1994), which were variable but averaged near 1:1. However, female-biased ratios have been reported in populations of *L. louisianensis* from the Louisiana coast in the northern Gulf of Mexico (Felder and

Lovett, 1989), as well as in populations of western Pacific intertidal thalassinideans such as *Trypaea australiensis* Dana (Hailstone and Stephenson, 1961), *Callianassa* s. l. *filholi* Milne Edwards (Devine, 1966), and sexually mature adult populations of *Neotrypaea californiensis* (Dana) and *Upogebia pugettensis* Dana (Dumbauld et al., 1996). Populations were male-biased in sampled populations of *Callianassa* s. l. *subterranea* Montagu from subtidal European waters (Rowden and Jones, 1994).

Observance of skewed sex ratios in thalassinidean samples may reflect actual bias in the population or an artifact of collecting methods that do not sample sexes equally within the vertical profile of burrows or across horizontal beach transections, especially when collections must be restricted to readily accessed reaches of shoreline sediments. Movement of ovigerous females toward the surface for egg release or to optimally ventilate eggs could lead to greater probability of their capture when burrows are aspirated with yabby pumps. Likewise, sampling restricted to shorelines may reflect differential positioning of sexes within the burrow along tidal or wave agitation clines. Such effects could account for previous observations in which populations of *Callichirus islagrande* were female-biased on high wave-energy beaches but not on nearby protected beaches, or for ratios that differed markedly from month to month in some populations of *L. louisianensis* from the Gulf of Mexico (Felder and Griffis, 1994). In the present study, mudflats along margins of drainage canals were fully accessible to sampling during periods of low pond discharge, samples were not limited to shorelines, and burrows were not as deep as reported for above mentioned populations of *C. islagrande* and *L. louisianensis*. From resin casts (Fig. 4 in Nates and Felder, 1998), it was observed that almost all burrows were <1 m in depth, thus encompassing water volumes readily extractable with yabby pumps.

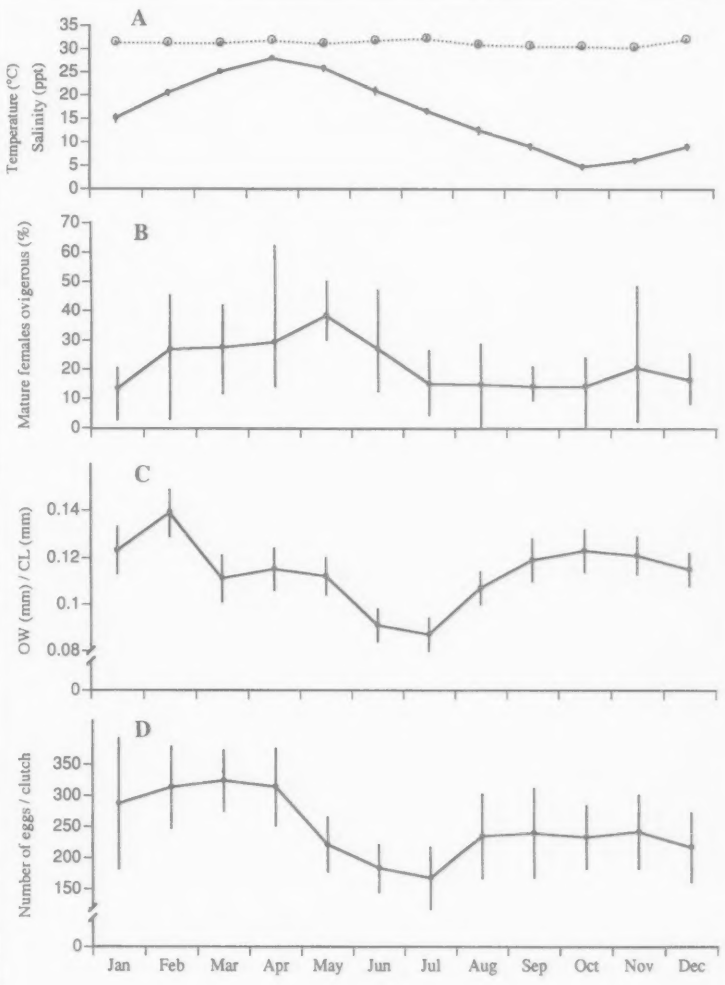


Figure 5

Pooled monthly measures for salinity, temperature, and reproductive indices in sampled Colombian populations of *Lepidophthalmus sinuensis*; for A, monthly temperature data were pooled from December 1991 through December 1993, and monthly salinity from January 1992 through December 1995; for B, monthly data were pooled from January 1992 through December 1995; for C, monthly data were pooled from January 1993 through December 1995; for A, C, and D, vertical lines define 95% CI; for B, vertical lines define range. (**A**) Morning surface salinity (solid circles, continuous line) at farm intake pump in upper estuary, and afternoon surface temperature (open circles, broken line) at outlet in pond 1, expressed as means of daily measures; (**B**) frequency of ovigerous individuals among mature (>11.0 mm CL) females of populations; (**C**) relative ovarian development (OW/CL); (**D**) mean number of eggs in clutches of ovigerous females.

Table 1

Formulae and statistics for linear regressions (by reduced major axis, with untransformed data) of chela width on carapace length (ChW:CL), chela height on carapace length (ChH:CL), chela width on chela height (ChW:ChH), total length on carapace length (TL:CL), and wet weight on carapace length (WW:CL) for male and female populations of *Lepidophthalmus sinuensis* sampled at the Agrosoledad S. A. shrimp farm, upper Cispata estuary, Colombia, from December 1991 through December 1995. Regressions were calculated for entire data set (All) and for data subdivided at the transition point (yielding separate regressions for data points $\leq X$ and data points $>X$, where X = size at onset of sexual maturity estimated by piecewise linear-linear polynomial regression), n = sample size, r^2 = coefficient of determination, 95% CI = confidence interval of slope.

	n	r^2	Formulae	95% CI
ChW:CL				
Males				
All	985	0.69	$ChW = (0.612 \times CL) - 3.474^{a}$	±0.021
$\leq X$	218	0.47	$ChW = (0.618 \times CL) - 3.179^{b}$	±0.061
$>X$	767	0.49	$ChW = (0.789 \times CL) - 5.974^{a,b}$	±0.039
Females				
All	1998	0.35	$ChW = (0.273 \times CL) - 0.519^{a,b}$	±0.009
$\leq X$	125	0.62	$ChW = (0.454 \times CL) - 1.925^{a,b}$	±0.049
$>X$	1873	0.12	$ChW = (0.304 \times CL) - 0.943^{a,b}$	±0.013
ChH:CL				
Males				
All	987	0.74	$ChH = (0.991 \times CL) - 4.843^{c}$	±0.031
$\leq X$	192	0.47	$ChH = (1.063 \times CL) - 5.012^{d}$	±0.111
$>X$	795	0.57	$ChH = (1.198 \times CL) - 7.761^{c}$	±0.054
Females				
All	1998	0.49	$ChH = (0.513 \times CL) - 0.425^{c,d}$	±0.016
$\leq X$	177	0.64	$ChH = (0.842 \times CL) - 3.345^{c,d}$	±0.075
$>X$	1821	0.20	$ChH = (0.513 \times CL) - 0.425^{c,d}$	±0.021
ChW:ChH				
Males				
All	987	0.94	$ChW = (0.618 \times ChH) - 0.482^{e,f}$	±0.009
$\leq X$	274	0.85	$ChW = (0.605 \times ChH) - 0.354^{g}$	±0.028
$>X$	713	0.88	$ChW = (0.655 \times ChH) - 0.831^{e,g}$	±0.017
Females				
All	2000	0.71	$ChW = (0.532 \times ChH) - 0.292^{e,g}$	±0.013
$\leq X$	71	0.88	$ChW = (0.550 \times ChH) - 0.175^{f}$	±0.046
$>X$	1929	0.53	$ChW = (0.588 \times ChH) - 0.646^{e}$	±0.018
TL:CL				
Males				
All	1007	0.80	$TL = (4.349 \times CL) - 1.033^{h,i,l}$	±0.121
$\leq X$	737	0.77	$TL = (4.693 \times CL) - 4.695^{h,l}$	±0.161
$>X$	270	0.15	$TL = (6.374 \times CL) - 32.918^{h,j}$	±0.703
Females				
All	2158	0.64	$TL = (4.641 \times CL) - 3.186i^{j,k}$	±0.117
$\leq X$	1006	0.64	$TL = (5.419 \times CL) - 11.495^{h,i,j}$	±0.201
$>X$	1152	0.22	$TL = (5.766 \times CL) - 19.813^{k}$	±0.293
WW:CL				
Males				
All	937	0.70	$WW = (0.751 \times CL) - 6.431^{l,m,o}$	±0.026
$\leq X$	200	0.22	$WW = (0.679 \times CL) - 5.250^{n}$	±0.084
$>X$	737	0.60	$WW = (0.998 \times CL) - 9.927^{l,n,s}$	±0.046
Females (including those with eggs)				
All	1933	0.49	$WW = (0.613 \times CL) - 5.053^{l,p}$	±0.019
$\leq X$	50	0.32	$WW = (0.508 \times CL) - 3.195^{m,q}$	±0.122
$>X$	1883	0.42	$WW = (0.698 \times CL) - 6.204^{l,p,q}$	±0.024
Females (excluding those with eggs)				
All	1542	0.53	$WW = (0.581 \times CL) - 4.680^{o}$	±0.019
$\leq X$	41	0.42	$WW = (0.472 \times CL) - 2.933^{l,n,r}$	±0.119
$>X$	1501	0.44	$WW = (0.662 \times CL) - 5.767^{o,r,s}$	±0.024

a–s = allometric coefficients with same superscript are significantly ($P<0.05$) different from each other.

Table 2

Allometric coefficients measured as slopes for linear regressions (by least squares estimate, with log-transformed data) of chela width on carapace length (ChW:CL), chela height on carapace length (ChH:CL), chela width on chela height (ChW:ChH), total length on carapace length (TL:CL), and wet weight on carapace length (WW:CL) for male and female populations of *Lepidophthalmus sinuensis* sampled at the Agrosoledad S. A. shrimp farm, upper Cispata estuary, Colombia, December 1991, through December 1995. Coefficients were determined for entire data set (All) and for data subdivided at the transition point (yielding separate regressions for data points $\leq X$ and data points $>X$, where X = size at onset of sexual maturity estimated by piecewise linear-linear polynomial regression), 95% CI = confidence interval of coefficient. * *= allometric coefficient significantly ($P<0.05$) different from 1.0. *a–u* = allometric coefficients with same superscript are significantly ($P<0.05$) different from each other.

	ChW:CL		ChH:CL		ChW:ChH		TL:CL		WW:CL	
	Allom. coef.	95% CI	Allom. coef.	95% CI	Allom. coef.	95% CI	Allom. coef.	95% CI	Allom. coef.	95% CI
Males										
All	1.577**^{a}	±0.059	1.457**^{e}	±0.047	1.085**^{i}	±0.017	0.928**^{m,q}	±0.027	3.094**^{s}	±0.118
$\leq X$	1.525**^{b}	±0.162	1.440**^{f}	±0.122	1.061**^{j}	±0.039	0.968^{n,r}	±0.035	2.762**	±0.747
$>X$	1.608**^{c}	±0.129	1.477**^{g}	±0.110	1.106**^{k}	±0.033	0.618**^{m,n,o}	±0.164	3.056**^{t}	±0.118
Females (including those with eggs)										
All	0.820**^{a,b,c,d}	±0.039	0.869**^{e,f,g,h}	±0.033	0.934**^{i,j,k,l}	±0.021	0.895**^{n,o,p}	±0.025	2.476**^{s,t}	±0.090
$\leq X$	1.625**^{d}	±0.210	1.470**^{h}	±0.160	1.096^{l}	±0.116	1.031^{m,o,p}	±0.052	3.458**^{u}	±1.102
$>X$	0.441**^{a,b,c,d}	±0.053	0.491**^{e,f,g,h}	±0.045	0.864**^{i,j,k,l}	±0.033	0.693**^{p,q,r}	±0.051	2.064**^{s,t,u}	±0.122

This observation suggests that the detected sex bias accurately characterizes the population sampled.

In the course of previously reported observations on populations of *C.* s. l. *filholi,* it was noted that the sex ratio was near 1:1 only when small animals were included in the sample (Devine, 1966). For *L. sinuensis* there is also a correlation between mean size of animals in the monitored population and sex ratio over the four years of monitoring. As noted for *C.* s. l. *filholi*, samples of smaller mean CL were nearer 1:1 in sex ratio than were samples of larger mean CL. The trend toward increasing frequency of females reached an approximate asymptote after 23 months of observation, simultaneous with the trend in increasing CL of males, and may indicate a point at which increasing numbers of larger males established a sexual equilibrium by displacing small males from a limited habitat or maintained territory. This increase corresponds roughly to the time when burrow densities within ponds on the farm began exponential increase and when detrimental effects on water quality and penaeid production became evident (equals month 38 in Figure 1 of Nates and Felder, 1998). Sex ratios and mean carapace lengths may thus serve to forecast potential for rapid increases in infesting populations.

Both the large body size and the robust chelipeds of mature males could be of advantage in competition for limited space and available females wherever *L. sinuensis* occurs in dense, mature aggregations. Such behaviors have been suggested previously to account for large numbers of possibly displaced juvenile males of *L. louisianensis* observed periodically in plankton samples (Felder and Lovett, 1989; Felder and Rodrigues, 1993). Similar intraspecific competition for space, in which juveniles are expelled to the surface, has also been postulated to occur in some populations of *Callianassa* s. l. *japonica* (Ortmann), along with possible immigration of juveniles to other habitats (Tamaki and Ingole, 1993). While not documented to occur in *L. sinuensis*, colonization of mariculture ponds by such displaced juvenile males pumped in with estuarine waters could account for higher percentages of males observed early in our study. Such recruitment of juveniles could potentially supplement larval settlement within ponds to rapidly build early infestation densities.

Ovigerous females

The abbreviated life cycle in *L. sinuensis* includes only two brief zoeal stages, large numbers of which occur in nocturnal plankton samples taken at the study site (Nates et al., 1997). The eggs of this species and its congener *L. louisianensis* are comparable in size to those of *Callianassa* s. l. *kraussi* Stebbing, another estuarine species that exhibits markedly abbreviated development (Forbes, 1973), and are larger than those of many thalassinids with longer larval histories and wider planktonic dispersal (see

Pohl, 1946; Forbes, 1973; Tunberg, 1986), with some clear exceptions (see de Vaugelas et al., 1986). Given abbreviated development in *L. sinuensis* and the likelihood of almost immediate settlement by decapodids into the vicinity of our sample site, we expected to detect distinct cohorts of small recruits, from which we could estimate rates of growth to maturation. However, unlike the population of the warm temperate species *L. louisianensis* from the Gulf of Mexico (Felder and Lovett, 1989), tropical populations of *L. sinuensis* included ovigerous females in every month of sampling. This potential for continuous recruitment over the annual cycle, coupled with our limited success in consistently capturing small individuals, limits clear definition of reproduction and growth cycles from collections of recruits.

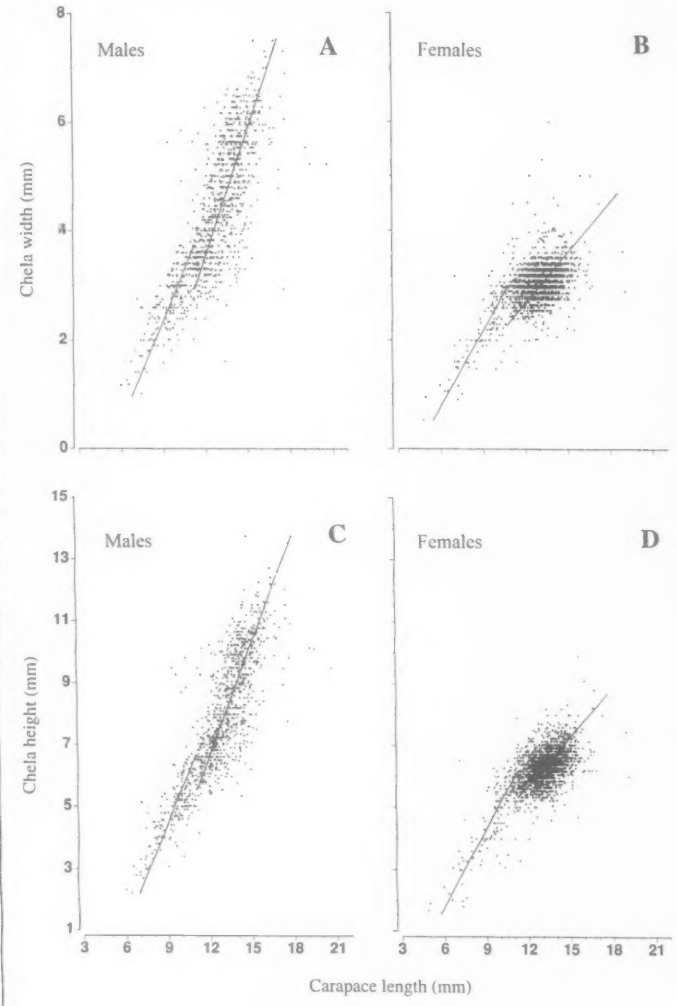


Figure 6

Linear regression (by least squares estimate for untransformed data) of chela width (ChW) on carapace length (CL) for (**A**) males and (**B**) females and chela height (ChH) on CL for (**C**) males and (**D**) females in sampled Colombian populations of *Lepidophthalmus sinuensis*, December 1991 through December 1995. The transition point at which data are subdivided, estimated by piecewise linear-linear polynomial regression, was positioned to minimize the sum of squares of residuals.

Vitellogenesis in *L. sinuensis* was evident in coloration and size changes of ovaries viewed through a translucent region of the cuticle, as in other thalassinid species (Hailstone and Stephenson, 1961; Forbes, 1977; Felder and Lovett, 1989). The pattern of change in *L. sinuensis* over the course of maturation is as much as that reported for *L. louisianensis*, with ovaries becoming more massive and opaque as maturation advances (Felder and Lovett, 1989). However, when tracked as an annual index of reproductive activity, relative ovarian width in *L. sinuensis* at no point reached the highest mean values reported for *L. louisianensis* (even after correcting misplaced decimals in the *y*-axis of Fig. 1 of Felder and Lovett [1989]). We suggest that this reflects year-round reproductive activity in *L. sinuensis*, rather than investment in a more punctuated temperature-modulated event as might be expected in temperate latitudes. It may also account for a greater number of eggs on ovigerous females of *L. louisianensis* (598 ±212; n=4) than on ovigerous females of the year-round reproducing *L. sinuensis* (251 ±18; n=444) (Nates et al., 1997). Even so, significant fluctuations in mean values for relative ovarian width did occur over the three years that we monitored this value in *L. sinuensis*, with highest values preceding maximum abundance of ovigerous females by two to three months.

In tropical nearshore decapods, it is common to have extended periods of reproduction without distinct peaks defined by seasonal temperature (Sastry, 1983; Steele, 1988; Bauer, 1992; Mouton and Felder, 1995). However, whether modulated by temperature or other factors, an-

nual cycles in availability of nutrition may determine potential for vitellogenesis and success of larvae (Zimmerman and Felder, 1991; Mouton and Felder, 1995). Although temperature was not subject to marked fluctuation in the shrimp farm habitat of *L. sinuensis*, it did vary slightly with the annual changes in rainfall patterns that determined salinity of the upper estuary (Fig. 4A). The annual decline in salinity from April through October reflected increased input of nutrient-loaded waters from the nearby Río Sinú which was reported to result in periodic elevation of penaeid shrimp growth rates on the Agrosoledad farm (Mogollón[1]). Similarly, such low salinity periods may have produced improved conditions for vitellogenesis in *L. sinuensis*. Peak development of ovaries in the first quarter of the typical year either coincided with or shortly followed lowest mean salinity during the last quarter of the previous year, and fell markedly just after salinity peaked. The abundance of ovigerous females peaked almost simultaneously with salinity in most years of the study and a decrease in mean ovarian width immediately followed, indicating that the abundance of females with spent ovaries was not offset by other females simultaneously undergoing vigorous ovarian development. Reduced vitellogenesis following the high salinity period was also suggested by the markedly reduced mean number of eggs per clutch found in those ovigerous females that occurred from May through July.

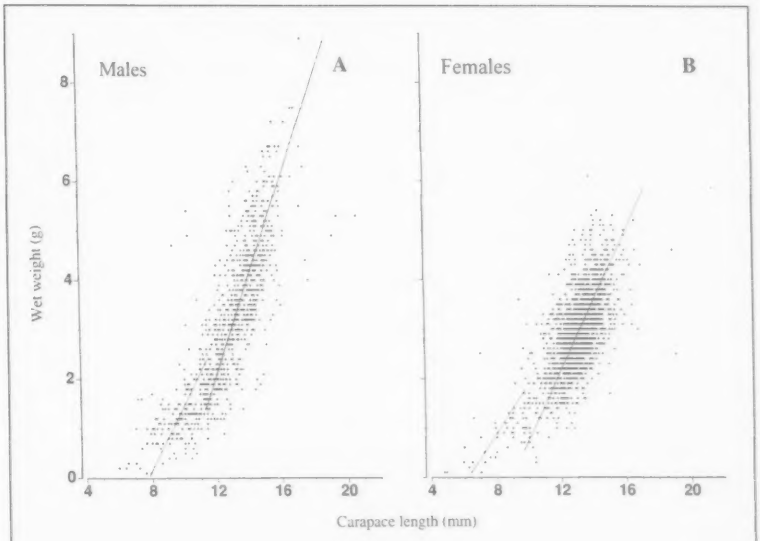


Figure 7

Linear regression (by least squares estimate for untransformed data) of wet weight (WW) on carapace length (CL) for males (**A**) and females (**B**) in sampled Colombian populations of *Lepidophthalmus sinuensis*, December 1991 through December 1995. The transition point at which data are subdivided, estimated by piecewise linear-linear polynomial regression, was positioned to minimize the sum of squares of residuals.

Growth and sexual maturation

Among callianassids and other thalassinid shrimp, the major chela is used commonly for aggressive interactions between captured individuals that are held together or among individuals encountering one another where burrows intersect in laboratory fossoria (MacGinitie, 1934; Pearse, 1945; Rodrigues, 1976; Tunberg, 1986; Felder and Lovett, 1989; Pillai, 1990; Rowden and Jones, 1994). Contrary to the case with many other genera, both males and females of *Lepidophthalmus* have one chela enlarged, but the major chela of mature males is much more strikingly developed than that of mature females (Felder and Rodrigues, 1993; Felder and Manning, 1997). Sexual dimorphism of the chelae in decapods is generally thought to reflect adaptations for their use, especially by males, in combat, display, and courtship (Hartnoll, 1974). The enlarged chela can play a role in intermale competition during the precopulatory phase of the life cycle, and marked change in its allometric growth rate is frequently related to functional sexual maturity (Grey, 1979; Aiken and Waddy, 1989; Claxton and Govind, 1994; Gu et al., 1994; Robertson and Kruger, 1994). This is likely also the case in *L. sinuensis*, even though we can only speculate as to the exact role this appendage plays in such fossorial populations.

A striking transition takes place in rate of relative growth for the major chela in *L. sinuensis*, and there is an allometric divergence between males and females in the shape of this appendage at sizes that exceed a defined, transitional carapace length. For the most part, the relationships of slopes above and below these transition or maturation points are similar to relationships previously reported in monitored

[1] Mogollón, J. V. 1995. Agrosoledad S. A., Playa de la Artillería no. 33–36, Cartagena, Columbia. Personal commun.

populations of *L. louisianensis* from the northern Gulf of Mexico (Felder and Lovett, 1989). In relative growth parameters of the major chela, when scaled to carapace length, males and females of both *Lepidophthalmus* species are much more similar to one another at sizes below transition points than at sizes exceeding those points.

The estimated maturational transition size in male *L. sinuensis* ranges from 11.0 to 11.3 mm CL, whether based upon regression analysis of relative growth in chela width, chela height, or wet weight. The range of these values is markedly less than that reported in *L. louisianensis* (≥15.5 mm CL), a warm-temperate congener (Felder and Lovett, 1989). In all of these measures, postmaturation growth rate in males is more positively allometric and significantly greater than postmaturation growth rate in females, as has been shown in many other decapods (Hartnoll, 1978, 1982). Although relative weight increases were positively allometric in both males and females of mature size, the positive allometry of growth in size of the major chela, accompanied by sex-dependent changes in its shape, appears to account for postmaturation rates of weight increase in males that significantly exceeding those of females. Weight accumulation due to massive but episodic development of ovaries in maturing females would appear to be somewhat offset by the simultaneous trend toward negative allometric growth of the major chela.

Estimated from the major chela measurements, the mean maturational size in female *L. sinuensis* ranges from 10.8 to 11.2 mm CL, or slightly less than that of males but very near the values reported for females of *L. louisianensis,* which ranged from 10.7 to 11.0 mm CL (Felder and Lovett, 1989). Because over 99% of the ovigerous females we collected were ≥11.0 mm CL, the general validity of this mean size estimate for maturation appears to be confirmed on an independent basis, even though two atypically small ovigerous females <10.0 mm CL, were collected (Fig. 4). Our regression analysis of wet weight indicated that the transitional maturation point for females fell near 9.8 mm CL, but error appeared to be high in values surrounding this point. A relatively large range and error in this weight-dependent value should perhaps be expected because two variables, negative allometry of the major chela and growth of the ovaries, are likely influencing it in opposite ways. We suggest that the aforementioned annual salinity variations and the simultaneous effects on nutrient loading may seasonally alter rates of ovarian growth. This could in turn contribute to the range of weight dependent values for maturation or account for occasional occurrences of small egg-bearing females by favoring early maturation of young cohorts.

Management summary

Those penaeid culture ponds on the Caribbean coast of Colombia that operate at higher salinities than those near the Río Sinú have not been found to harbor detrimental infestations of *Lepidophthalmus*. However, nutrient-rich, estuarine waters are believed to yield high rates of penaeid production, promoting location of several major penaeid farms in oligohaline habitats that harbor natural populations of *L. sinuensis*. This pest is introduced to culture ponds by pumping in larvae and perhaps migrant juveniles from the estuary. Although filtration of influent water should serve to limit entry of any migrant juveniles, it is practical to limit entry of much smaller planktonic larvae only by carefully avoiding pumping in of waters from the estuary during nocturnal hours of peak larval activity in the water column (Nates et al., 1997). Because we herein document that *L. sinuensis* reproduces year-round, this diel restriction of pumping schedules cannot be limited solely to the first annual quarter of elevated salinity when peak abundances of ovigerous females suggest that high densities of larvae might be present among nocturnal plankton. However, such periods would almost certainly present the greatest risk of larval introductions to culture ponds.

Although controlling water influx may limit colonization of ponds from surrounding environments, *Lepidophthalmus* will almost certainly over time succeed in becoming established in estuarine ponds that provide it with both richly organic muddy substrates and annual cycles of water quality that favor reproduction. Detrimental effects become obvious when densities in ponds exceed 200 burrow openings/m^2 or 66 animals/m^2 (Nates and Felder, 1998), levels we have never found in natural settings on in the Río Sinú estuary. Explosive reproduction within the ponds appears to immediately precede problem levels of infestation, and measurements of the sex ratios and CL of the population may serve to forecast the potential for such an event. Because attainment of a strongly female-biased sex ratio is roughly coincident with previously reported exponential population growth (Nates and Felder, 1998), both sex ratio and density of mature females may prove useful predictors of population growth potential. Maturity of both males and females can be determined by measures of CL and cheliped dimensions, or by inference from burrow diameters, and immediately pending episodes of egg deposition can be predicted by monitoring the ovarian index.

Dense infestations of *Lepidophthalmus* in Colombian shrimp culture ponds have to date been treated periodically by farm operators with the carbaryl pes-

ticide Sevin®, a practice unlikely to change in the absence of proven alternative management strategies. From our observations, such applications have usually been contained within drained or slightly filled culture ponds and limited only to control of excessive thalassinid densities. It is possible that reductions in frequencies of such applications can be achieved by timing of treatments to pre-empt reproductive peaks or by limiting pesticide applications only to infestations that are found to include high percentages of mature or near-mature females, such as we observed in this study most often in the fourth annual quarter. Any measure that reduces application rates and frequencies may lessen ecological risks and contribute to effectiveness of carbaryl degradation prior to flushing treated ponds into surrounding environments.

Acknowledgments

We thank G. T. Rizzuto, R. G. Jaeger, P. L. Klerks, and R. R. Twilley, University of Southwestern Louisiana, and R. Lemaitre, Smithsonian Institution, for comments on earlier versions of the manuscript. We are also grateful to many associates of the Agrosoledad S. A. shrimp farm, particularly J. V. Mogollón, L. Mogollón, G. Moreno, and M. Torralvo, who provided access to sites in Colombia, and A. Arroyo, D. Espitia, and S. Garcia, who assisted in collecting population data there. Among others who assisted with field and laboratory work, we thank L. Borda, R. Bourgeois, V. Fuentes, R. Griffis, R. Lemaitre, C. Moreau, S. de A. Rodrigues, and K. Strasser. Fellowship support for this project was provided to S. F. Nates from the Instituto Colombiano para el Desarrollo de la Ciencia y la Tecnología Francisco José de Caldas (COLCIENCIAS), Colombia. Logistical support was provided through ACUANAL, BANCOLDEX, and the efforts of C. M. Sanín. Support was provided to D. L. Felder through U.S. Minerals Management Service Cooperative Agreement 14-35-0001-30470, U.S. Fish and Wildlife Service Cooperative Agreement 14-16-0009-89-96—Task Order No. 6, NOAA Louisiana Sea Grant College Program Grant R/CFB-21, and U.S. Department of Energy Grant No. DE-FG02-97ER12220.

Literature cited

Aiken, D. E., and S. L. Waddy.
1989. Allometric growth and onset of maturity in male American lobsters (*Homarus americanus*): the crusher propodite index. J. Shellfish Res. 8:7–11.

Bauer, R. T.
1992. Testing generalization about latitudinal variation in reproduction and recruitment patterns with sicyoniid and caridean shrimp species. Invertebr. Reprod. Dev. 22:193–202.

Claxton, W. T., and C. K. Govind.
1994. Chela function, morphometric maturity, and the mating embrace in male snow crab, *Chionoecetes opilio*. Can. J. Fish. Aquat. Sci. 51:1110–1118.

Devine, C. E.
1966. Biology of *Callianassa filholi* Milne-Edwards 1878 (Crustacea, Thalassinidea). Trans. R. Soc. N.Z., Zool. 8:93–110.

Dumbauld, B. R., D. A. Armstrong, and K. L. Feldman.
1996. Life-history characteristics of two sympatric thalassinidean shrimps, *Neotrypaea californiensis* and *Upogebia pugettensis*, with implications for oyster culture. J. Crust. Biol. 16:689–708.

Felder, D. L.
1978. Osmotic and ionic regulation in several western Atlantic Callianassidae (Crustacea, Decapoda, Thalassinidea). Biol. Bull. 154:409–429.
1979. Respiratory adaptations of the estuarine mud shrimp, *Callianassa jamaicense* (Schmitt, 1935) (Crustacea, Decapoda, Thalassinidea). Biol. Bull. 157:125–137.

Felder, D. L., and R. B. Griffis.
1994. Dominant infaunal communities at risk in shoreline habitats: burrowing thalassinid Crustacea. Outer Continental Shelf (OCS) Study MMS 94-0007. U.S. Dep. Interior, Minerals Manage. Service, Gulf of Mexico OCS Regional Office, New Orleans, LA, 87 p.

Felder, D. L., and D. L. Lovett.
1989. Relative growth and sexual maturation in the estuarine ghost shrimp *Callianassa louisianensis* Schmitt, 1935. J. Crust. Biol. 9:540–553.

Felder, D. L., and R. B. Manning.
1997. Ghost shrimps of the genus *Lepidophthalmus* from the Caribbean region, with description of *L. richardi*, new species, from Belize (Decapoda: Thalassinidea: Callianassidae). J. Crust. Biol. 17:309–331.

Felder, D. L., and S. de A. Rodrigues.
1993. Reexamination of the ghost shrimp *Lepidophthalmus louisianensis* (Schmitt, 1935) from the northern Gulf of Mexico and comparison to *L. siriboia*, new species, from Brazil (Decapoda: Thalassinidea: Callianassidae). J. Crust. Biol. 13:357–376.

Felder, J. M., D. L. Felder, and S. C. Hand.
1986. Ontogeny of osmoregulation in the estuarine ghost shrimp *Callianassa jamaicense* var. *louisianensis* Schmitt (Decapoda, Thalassinidea). J. Exp. Mar. Biol. Ecol. 99:91–105.

Forbes, A. T.
1973. An unusual abbreviated larval life in the estuarine prawn *Callianassa kraussi* (Crustacea: Decapoda: Thalassinidea). Mar. Biol. 22:361–365.
1974. Osmotic and ionic regulation in *Callianassa kraussi* Stebbing (Crustacea, Decapoda, Thalassinidea). J. Exp. Mar. Biol. Ecol. 16:301–311.
1977. Breeding and growth of the burrowing prawn *Callianassa kraussi* Stebbing (Crustacea, Decapoda, Thalassinidea). Zool. Afr. 12:149–161.
1978. Maintenance of non-breeding populations of the estuarine prawn *Callianassa kraussi* (Crustacea, Anomura, Thalassinidea). Zool. Afr. 13:33–40.

Grey, K. A.
1979. Estimates of the size of first maturity of the western

rock lobster, *Panulirus cygnus*, using secondary sexual characteristics. Aust. J. Mar. Freshwater Res. 30:785–791.

Gu, H., P. B. Mather, and M. F. Capra.
1994. The relative growth of chelipeds and abdomen and muscle production in male and female redclaw crayfish, *Cherax quadricarinatus* von Martens. Aquaculture 123:249–257.

Hailstone, T. S., and W. Stephenson.
1961. The biology of *Callianassa* (Trypaea) *australiensis* Dana 1852 (Crustacea, Thalassinidea). Univ. Queensl. Pap. Dep. Zool. 1(12):259–285.

Hartnoll, R. G.
1974. Variation in growth pattern between some secondary sexual characters in crabs (Decapoda Brachyura). Crustaceana 27:131–136.
1978. The determination of relative growth in Crustacea. Crustaceana 34:281–293.
1982. Growth. *In* L. G. Abele (ed.), The biology of Crustacea, vol. 2, Embryology, morphology, and genetics, p. 111–116. Academic Press, New York, NY.

Hintz, J. L.
1995. NCSS 6.0.1–3 user's manuals I–III. Number Cruncher Statistical Systems, Kaysville, UT, 2204 p.

Huxley, J. S.
1932. Problems of relative growth. Dial Press, New York, New York, NY, 276 p.

Lemaitre, R., and S. de A. Rodrigues.
1991. *Lepidophthalmus sinuensis*: A new species of ghost shrimp (Decapoda: Thalassinidea: Callianassidae) of importance to the commercial culture of penaeid shrimps on the Caribbean coast of Colombia, with observations on its ecology. Fish. Bull. 89:623–630.

Lovett, D. L., and D. L. Felder.
1989. Application of regression techniques to studies of relative growth in crustaceans. J. Crust. Biol. 9:529–539.

MacGinitie, G. E.
1934. The natural history of *Callianassa californiensis* Dana. Am. Midl. Nat. 15:166–177.

Manning, R. B.
1975. Two methods for collecting crustaceans in shallow water. Crustaceana 29:317-319.

Manning, R. B., and D. L. Felder.
1990. Revision of the American Callianassidae (Crustacea: Decapoda: Thalassinidea). Proc. Biol. Soc. Wash. 104:764–792.

McEdward, L. R., and F. Chia.
1991. Size and energy content of eggs from echinoderms with pelagic lecithotrophic development. J. Exp. Mar. Biol. Ecol. 147:95–102.

Mouton, E. C., Jr., and D. L. Felder.
1995. Reproduction of the fiddler crabs *Uca longisignalis* and *Uca spinicarpa* in a Gulf of Mexico salt marsh. Estuaries 18:468–481.

Mukai, H., and I. Koike.
1984. Behavior and respiration of the burrowing shrimps *Upogebia major* (De Haan) and *Callianassa japonica* (De Haan). J. Crust. Biol. 4:191–200.

Nates, S. F., and D. L. Felder.
1998. Impacts of burrowing ghost shrimp, genus *Lepidophthalmus*, on penaeid shrimp culture (Crustacea: Decapoda: Thalassinidea). J. World Aqua. Soc. 29:189–211.

Nates, S. F., D. L. Felder, and R. Lemaitre.
1997. Comparative larval development in two species of the burrowing ghost shrimp genus *Lepidophthalmus* (Crustacea: Decapoda: Callianassidae). J. Crust. Biol. 17:497–519.

Pearse, A. S.
1945. Ecology of *Upogebia affinis* (Say). Ecology 26:303–305.

Phillips, P. J.
1971. Observations on the biology of mudshrimps of the genus *Callianassa* (Anomura: Thalassinidea) in Mississippi Sound. Gulf Res. Rep. 3:165–196.

Pillai, G.
1990. Notes on the chelae of the mangrove-lobster *Thalassina anomala* (Decapoda, Thalassinidae). Crustaceana 59:87–95.

Pohl, M. E.
1946. Ecological observations on *Callianassa major* Say at Beaufort, North Carolina. Ecology 27:71–80.

Poore, G. C. B., and T. H. Suchanek.
1988. *Glypturus motupore*, a new callianassid shrimp (Crustacea: Decapoda) from Papua New Guinea with notes on its ecology. Rec. Aust. Mus. 40:197–204.

Posey, M. H.
1987. Effects of lowered salinity on activity of the ghost shrimp *Callianassa californiensis*. Northwest Sci. 61:93–96.

Robertson, W. D., and A. Kruger.
1994. Size at maturity, mating and spawning in the portunid crab *Scylla serrata* (Forskål) in Natal, South Africa. Estuarine Coastal Shelf Sci. 39:185–200.

Rodrigues, S. de A.
1976. Sobre a reprodução, embriologia e desenvolvimento larval de *Callichirus major* Say, 1818 (Crustacea, Decapoda, Thalassinidea). Bolm. Zool., Univ. S. Paulo 1:85–104.

Rowden, A. A., and M. B. Jones.
1993. Critical evaluation of sediment turnover estimates for Callianassidae (Decapoda: Thalassinidea). J. Exp. Mar. Biol. Ecol. 173:265–272.
1994. A contribution to the biology of the burrowing mud shrimp, *Callianassa subterranea* (Decapoda: Thalassinidea). J. Mar. Biol. Assoc. (U.K.) 74:623–635.
1995. The burrow structure of the mud shrimp *Callianassa subterranea* (Decapoda: Thalassinidea) from the North Sea. J. Nat. Hist. 29:1155–1165.

Sastry, A. N.
1983. Ecological aspects of reproduction. *In* J. F. Vernberg and W. B. Vernberg (eds.), The biology of Crustacea, vol. 8, Environmental adaptations, p. 179–270. Academic Press, New York, NY.

Steele, D. H.
1988. Latitudinal variations in body size and species diversity in marine decapod crustaceans of the continental shelf. Int. Rev. Gesamten. Hydrobiol. 73:235–246.

Tamaki, A., and B. Ingole.
1993. Distribution of juvenile and adult ghost shrimps, *Callianassa japonica* Ortmann (Thalassinidea), on an intertidal sand flat: intraspecific facilitation as a possible pattern-generating factor. J. Crust. Biol. 13:175–183.

Thompson, R. K., and A. W. Pritchard.
1969. Respiratory adaptations of two burrowing crustaceans, *Callianassa californiensis* and *Upogebia pugettensis* (Decapoda, Thalassinidea). Biol. Bull. 136:247–287.

Tunberg, B.
1986. Studies on the population ecology of *Upogebia deltaura* (Leach)(Crustacea, Thalassinidea). Estuarine Coastal Shelf Sci. 22:753–765.

Vaugelas, J. de, B. Delesalle, and C. Monier.
1986. Aspects of the biology of *Callichirus armatus* (A. Milne Edwards, 1870) (Decapoda, Thalassinidea) from French Polynesia. Crustaceana 50:204–216.

Witbaard, R., and G. C. A. Duineveld.
1989. Some aspects of the biology and ecology of the burrowing shrimp *Callianassa subterranea* (Montagu) (Thalassinidea) from the Southern Sea. Sarsia 74:209–219.
Ziebis, W., S. Forster, M. Huettel, and B. Jørgensen.
1996. Complex burrows of the mud shrimp *Callianassa truncata* and their geochemical impact in the sea bed. Nature 382:619–622.
Zimmerman, T. L., and D. L. Felder.
1991. Reproductive ecology of an intertidal brachyuran crab, *Sesarma* sp. (nr. *reticulatum*), from the Gulf of Mexico. Biol. Bull. 181:387–401.

Capture rate as a function of school size in pantropical spotted dolphins, *Stenella attenuata*, in the eastern tropical Pacific Ocean

Peter C. Perkins

Elizabeth F. Edwards

Southwest Fisheries Science Center
8604 La Jolla Shores Dr.
La Jolla, California 92038
E-mail address (for P. C. Perkins): peter@caliban.ucsd.edu

Abstract.–The frequency with which dolphins from the northeastern offshore stock of the pantropical spotted dolphin, *Stenella attenuata*, experience chase and capture by tuna purse-seiners in the eastern topical Pacific Ocean was estimated by comparing dolphin school-size frequencies in sighting data from research vessel observer records, with those recorded in set data by tuna vessel observers. The objective of the study was to provide a preliminary basis for estimating stock-wide effects of fishery-induced disturbance in these dolphins.

Our analyses indicate two major characteristics for this stock: first, capture frequency appears to increase rapidly with increasing school size, and second, approximately half of the stock at any given time occurs in schools smaller than those apparently preferred by purse-seiners. This implies that if individual dolphins have a preference for associating with schools of a particular size, then individuals associating primarily with large schools would be subjected to chase and capture much more frequently than those associating with small schools. However, because the largest schools are relatively rare and account for a small percentage of individuals, the majority of dolphins in the stock would experience relatively few captures per year, although some would experience a high rate. It is not known whether dolphins do indeed exhibit such a preference, or if instead individuals associate with schools from a wide range of sizes at different times.

Schools of 1000 or more dolphins are estimated to be set on approximately once a week each on average, but such schools are estimated to represent just under one tenth of the animals in the northeastern offshore stock. Schools set on most often by tuna purse-seiners, containing from about 250 to 500 dolphins, are estimated to be set on between two and eight times each per year and are estimated to include approximately one third of the stock. An estimated one half of the stock occurs in schools smaller than 250 animals; schools of this size are estimated to be set on less than twice per year each.

Manuscript accepted 20 July 1998.
Fish. Bull. 97:542–554 (1999).

Tuna fishermen in the eastern tropical Pacific Ocean (ETP) commonly catch large yellowfin tuna (*Thunnus albacares*) by locating a school of dolphins visually and then surrounding it with a large purse-seine net in order to capture the tuna that are often closely associated with ETP dolphin schools. The dolphins are released from the net and the tuna are then loaded aboard (NRC, 1992). This method, known as "fishing on dolphin," historically has been a significant cause of dolphin mortality (NRC, 1992) but has also recently been suggested as a significant cause of fishery-related physiological stress in the dolphins involved, perhaps to the point of causing unobserved mortality or changes in reproductive success (e.g. Myrick and Perkins, 1995).

Although it has not been possible to measure physiological stress directly in these dolphins, it is possible to use existing data to estimate how often an animal experiences chase and capture. Capture frequency provides at least a rough measure of the amount of fishery-induced disturbance that dolphins affected by the ETP tuna fishery experience. Here, we estimate capture frequency for the northeastern offshore stock of the pantropical spotted dolphin (*Stenella attenuata*) (Dizon et al., 1992). This is the species most commonly associated with tuna and historically most often used in fishing on dolphin (greater than 70% of dolphin sets annually for about the last 30 years (e.g. IATTC[1]).

A simple calculation (see "Discussion" section) leads to a rough estimate for the mean number of times an individual dolphin is set on per year of (number of dolphins set on) ÷ (number of dolphins) ≈ 8 times per year. However, simply knowing the overall average rate of capture is not sufficient to evaluate the potential adverse effects on individuals because the rate for different animals may vary widely, depending on a number of interrelated factors including school size, geographic location, time of year, and the amount of tuna associated with a school. In this paper, we investigate the effects of school size. Specifically, we show that large dolphin schools (more than several hundred animals) are much more likely to be captured than are small schools (less than one hundred animals) because of a tendency for fishermen to concentrate their effort on larger schools, which tend to carry more tuna, and to virtually ignore smaller ones. However, this result does not directly give the capture rate for an

[1] IATTC. 1992. Annual report: 1990. Inter-American Tropical Tuna Commission, La Jolla, CA, 261 p.

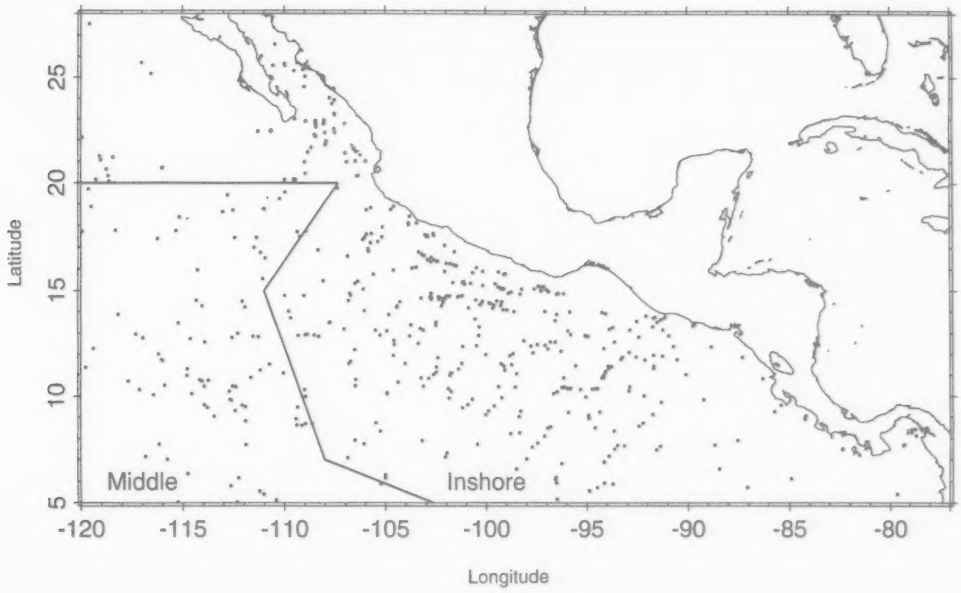


Figure 1

Geographic stock boundaries for the northeastern offshore stock of the pantropical spotted dolphin (*Stenella attenuata*). The stock is defined by the region in the ETP north and east of 5°N and 120°W, bounded at 28°N. The two strata pictured are based on those defined by Holt et al. (1987). The inshore and middle strata have total areas of 4,544,000 km^2 and 2,019,000 km^2, respectively. Points represent on-effort sightings from the research vessels, 1986–90 and 1992–93.

individual dolphin because animals may associate with schools of different sizes at different times. We consider implications for individual dolphins in the "Discussion" section.

Data and methods

To quantify the tendency for purse-seiners to set on large schools, we compared the relative frequency with which different sizes of schools are selected by fishermen for encirclement with the relative frequency with which schools of various sizes occur naturally. First, we estimated the probability distribution of sizes for spotted dolphin schools within the geographic boundaries of the northeast (NE) offshore stock[2] (Fig. 1), using observations from research vessels. This distribution models the relative number of schools of each size in the study area. Then we fitted a smooth probability distribution to dolphin school sizes from tuna vessel sets. This distribution models the relative number of times schools of each size were set on. Finally, we used the ratio of the two estimated density functions, suitably scaled, to estimate the average number of times per year a dolphin school of a given size was set on. This estimated effect includes not only the tendency of fishermen to preferentially set on larger schools, but also any tendency to search in areas where large schools may be more prevalent.

Research vessel sighting data

In 1986, the U.S. National Marine Fisheries Service (NMFS) initiated a multiyear research program to monitor trends in the abundance of dolphin populations in the ETP. The program used research vessels to conduct line transect surveys in the ETP and record sightings of all cetaceans encountered (Wade and Gerrodette, 1993). The surveys were designed to provide a spatially unbiased sample of the survey area and to be as similar as possible across years. Typically, three independent observers estimated school size and species composition for each sighting. For detailed descriptions of the survey design, materials, and methods, see Holt et al. (1987), Hill et al. (1991), and Mangels and Gerrodette (1994).

The research vessel data used in this study consisted of spotted dolphin school sightings from the

[2] Coastal and NE Offshore stocks of the pantropical spotted dolphin exist sympatrically: however, schools are for the most part distinguishable.

Table 1

Summary of research vessel data by year and stratum. Search effort is defined as the distance travelled along the trackline as observers actively search during a sea state of Beaufort 5 or less. Sighting rate is defined as the number of northeastern offshore spotted dolphin schools sighted on-effort, within 5.5 km of the ship's trackline, per 1000 km of search effort. Middle and inshore strata are defined in Figure 1.

	Inshore stratum		Middle stratum		Pooled	
Year	Search effort (km)	Sighting rate	Search effort (km)	Sighting rate	Search effort (km)	Sighting rate
1986	9260	6.26	3457	4.92	12,716	5.90
1987	8523	7.27	4322	5.09	12,845	6.54
1988	6303	6.98	3371	3.26	9674	5.69
1989	8375	9.67	3996	4.00	12,371	7.84
1990	7036	8.10	4744	3.79	11,780	6.37
1992	10,189	5.99	0	—	10,189	5.99
1993	7953	6.29	584	3.42	8537	6.09

1986–90 and 1992–93 marine mammal surveys (Table 1). These seven surveys each occurred between 28 July and 10 December, referred to here as the "study period." We used sightings only from search effort within the NE offshore stock boundaries, for which observers were actively searching ("on-effort") and for which Beaufort sea state was 5 or below. We excluded sightings farther than 5.5 km from the trackline because school size estimates were generally unreliable for such distant schools. A total of 499 sightings were included in this study.

The median estimated school size was 106 dolphins; 48% of the estimates were less than 100, and only 1% greater than or equal to 1000 (Fig. 2A). These quantities are not corrected for size selection bias (see "Statistical model" section). The true distribution of school sizes was estimated to include a larger percentage of small schools.

Tuna vessel set data

Since the late 1970s, the Inter-American Tropical Tuna Commission (IATTC) and NMFS have placed trained observers aboard a significant percentage of ETP tuna purse-seiner vessels larger than 400 tons capacity. A single observer is placed aboard a vessel when a trip is selected for observation. These observers collect data on the dolphins with which commercial species of tuna in the ETP commonly associate, and monitor dolphin mortality due to purse-seine fishing operations. For a more detailed description of the observation programs, see IATTC (1989), IATTC,[1] or Jackson (1993).

Detailed observer data were available from tuna sets made by U.S. vessels. From these data, we used observer estimates of school size and species composition from spotted dolphin schools set on by tuna vessels within the NE offshore stock boundaries and during the study period for the years 1986–90. We used the observer's final "best" estimates, made after the set, which included counts of any animals that evaded or were cut out of net encirclement[3] (IATTC, 1991; NMFS, 1992). The tuna vessel data used here included only schools that were actually set on, and not observations of schools that were sighted but not set on. We assumed that there was no "observer effect" on a captain's choice of schools to be set on. A total of 3454 set observations were included in this study (Table 2).

The tuna vessel set data represent about 77% of the search effort during the study period for the U.S. purse-seine fleet (29 to 40 vessels during the years 1986–90). To increase search efficiency, tuna vessels often travel at 15 knots, and crews use helicopters and communicate in "code groups" (Orbach, 1977) in addition to searching with binoculars from the ship. Not all schools that are sighted are set upon, and thus the observed sets represent a much larger effective sample size in terms of sightings, and the "missing" schools tend to be small. The median estimated size of schools that were set upon was 560 dolphins. Only 4% of the estimates were less than 100, whereas 26% were greater than or equal to 1,000 (Fig. 2B).

[3] Using the pre-encirclement school size means that although we are estimating the rate at which schools of a given size were set on, it is likely that some dolphins involved in a given set were chased by the tuna vessel and its speedboats but not actually encircled by the purse-seine net. For the purposes of estimating numbers of sets as a measure of adverse impact, we do not distinguish chase from capture.

Data from individual sets made by non-U.S. vessels were not available; however, count data summarizing observed numbers of sets and trips made by all vessels were available. From these data, we used the numbers of sets on the target stock observed each year, by both U.S. and non-U.S. vessels, during the study period and for the entire year (Table 2). Additionally, the total annual number of fishing trips that involved sets on dolphins has been estimated each year from tuna vessel logbook data (e.g. IATTC[1]). Dividing the annual number of observed trips by the annual total number of trips gives the annual trip sampling fraction ("coverage"), which we took as known exactly. We further assumed that observer coverage was constant throughout the year and took the sampling fractions as applicable for the study period as well as the entire year.

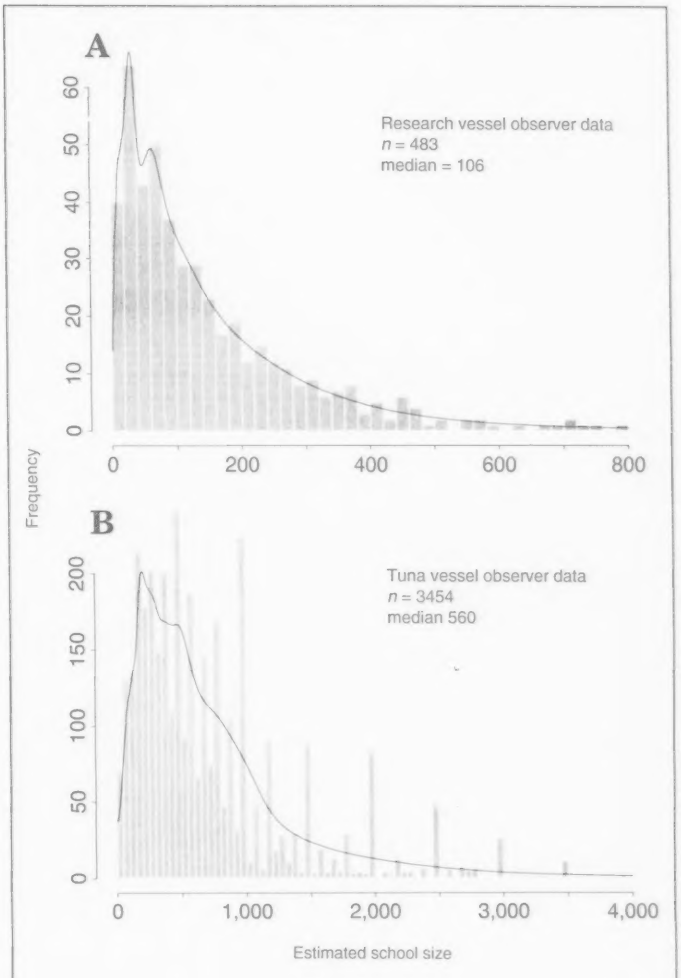


Figure 2

Estimated observed school sizes for northeastern offshore spotted dolphins. These data include observations from both geographic strata. The fitted lines are kernel density estimates (see text) for these observations. Note the different x- and y-axis scalings. (**A**) Research vessel sightings, 1986–90 and 1992–93. These data are the mean observer estimates and are not corrected for size selection bias (see text). They include on-effort sightings with perpendicular distance <5.5 km; 8 observations >800 are not shown. (**B**) Tuna vessel sets, 1986–90; 19 observations >4000 not shown.

Statistical model

We modeled the true population of NE offshore spotted dolphin schools within the stock boundaries as an independent identically distributed (i.i.d.) sample of unknown size from a hypothetical infinite superpopulation of schools having a smooth probability density for their school sizes. To characterize the true population of school sizes, both the total number of schools, $N_{schools}$, and the probability density from which their school sizes were drawn, $\pi(s)$, needed to be estimated. Although school size is really a discrete quantity, we approximated it using a continuous-valued random variate.

Dolphin school sightings are made from visual clues such as surface disturbances or associated bird flocks, and larger schools in general provide a more visible target. Thus, the sighting probability for schools at a given range depends on school size, leading to a selection bias (relative to $\pi(s)$) towards larger schools in the research vessel observations. We modeled these observations as a biased sample of size $n_{schools}$ from the true population. Because the ships' tracklines were random with respect to the dolphin population, we assumed that there were no other selection biases. We denoted the probability density of observed school sizes by $\pi^*(s)$ to distinguish it from $\pi(s)$, and note that

$$\pi(s) = \frac{w_{eff}}{w_{eff}(s)} \pi^*(s),$$

where $w_{eff}(s)$ = the line transect effective strip halfwidth for schools of size s ; and

w_{eff} = the size-averaged effective strip halfwidth (Appendix D in Burnham et al., 1980).

Table 2

Summary of tuna vessel data by fleet, year, and stratum. Coverage is defined as the percentage of fishing trips, involving sets on dolphins by vessels over 400 tons, that carried a scientific observer. Coverages and annual numbers of trips are taken from IATTC Annual Reports (e.g. IATTC, see Footnote 1 in main text). Observed sets per trip is defined as the mean number of observed sets on northeastern offshore spotted dolphin schools for trips that involved sets on dolphins. Middle and inshore strata are defined in Figure 1.

			Observed sets per trip 28 Jul–10 Dec ("study period")				Observed sets per trip annual			
Fleet	Year	Coverage	Trips	Inshore	Middle	Pooled	Trips	Inshore	Middle	Pooled
U.S.	1986	41.7	25	9.60	1.96	11.6	43	14.4	4.53	18.9
	1987	91.5	61	17.3	5.25	22.6	119	21.9	6.89	28.8
	1988	57.6	33	13.7	4.88	18.6	76	13.0	4.86	17.9
	1989	99.1	50	14.9	3.66	18.6	115	15.3	3.77	19.1
	1990	100.0	14	16.3	3.21	19.5	73	12.3	3.62	15.9
	Total	76.9	183	14.9	4.14	19.0	426	16.2	4.88	21.1
Intl.	1986	25.3	29	12.3	2.90	15.2	68	14.9	2.84	17.7
	1987	28.3	44	15.8	0.409	16.2	82	17.9	0.988	18.9
	1988	35.8	54	8.70	3.52	12.2	111	10.3	3.87	14.2
	1989	37.0	57	13.6	2.61	16.2	141	13.3	2.41	15.7
	1990	42.0	66	8.35	6.92	15.3	147	12.3	4.77	17.1
	Total	34.3	250	11.4	3.60	15.0	549	13.3	3.18	16.5

Both $w_{eff}(s)$ and w_{eff} depend upon the data truncation distance (Burnham et al., 1980), denoted by w and equal to 5.5 km in this analysis. $\pi^*(s)$ was estimated from the observed school sizes. However, to estimate $\pi(s)$, we also needed to estimate $w_{eff}(s)$, as described in "Estimation" section.

Anecdotal reports consistently imply that tuna vessel captains do not search for or set on dolphin schools at random when fishing on dolphin in the ETP. Because larger dolphin schools are observed to carry more tuna, they are presumably sought out and set upon preferentially, and the set data would have a selection bias towards large schools. We modeled the schools associated with purse-seine sets (both observed and unobserved) as a biased sample, with replacement, of unknown size from the true population of schools. To characterize these schools, both the total number of sets, N_{sets}, and the effective probability density from which their sizes were drawn, $p(s)$, needed to be estimated. $p(s)$ represents the superposition of the tuna fishermen's school-size selection preference upon $\pi(s)$. Sizes were recorded for all sets on trips carrying observers, and therefore there was no additional observer selection bias (in relation to $p(s)$). Assuming a random selection of trips, we treated the observed sets as an unbiased subsample of size n_{sets} and estimated $p(s)$ directly from the observed sizes. There was some concern with serial correlation between sets (see "Independence of observations" section).

Because the number of dolphin schools is not constant over time, we interpreted $N_{schools}$ as the time-averaged expected number of schools, and in particular did not use a finite population estimator. Similarly, we interpreted N_{sets} as the expected number of sets rather than making finite population estimates of the actual realized number of sets.[4]

Estimation

U.S. vessels—study period The observed school-size distributions from both the research vessel sighting data and from the tuna vessel set data were roughly lognormal in shape (Fig. 2). We estimated $\pi^*(s)$ and $p(s)$ using an adaptive kernel density estimator on the logs of the observed school sizes and then transformed the estimated density back to the original scale (Silverman, 1986). This variable bandwidth algorithm was chosen in order to make reasonable density estimates in the right tails where there were few data, while not oversmoothing near the modes. We chose the bandwidth scaling parameters as a trade-off between smoothness and fit to the data. We treated the observer estimates (mean estimates in the case of research vessel data) as exact measure-

[4] Technical details and a discussion of our estimators for $N_{schools}$ and N_{sets} can be found in Perkins, P. C., and E. F. Edwards, 1997, SWFSC Admin. Rep. LJ-97-03, Southwest Fisheries Science Center, La Jolla CA, 36 p.

ments and did not attempt to correct for the possibility of size estimation biases in either data set (see "Discussion" section) or use a deconvolution kernel to account for estimation variance.

Our estimates of $w_{eff}(s)$ were based on modelling the inherent selection bias in the research vessel sighting data. We used a bivariate hazard-rate detection function in a size-dependent line transect analysis of the perpendicular sighting distances and sizes of the observed schools (Drummer and McDonald, 1987; Palka, 1993). Perpendicular distances were binned to reduce the effect of rounding in the data. School sizes were not binned because we did not use a parametric model for their distribution.

We define the average capture frequency for a school of size s as

$$N_{capture}(s) = \frac{N_{sets}(s)}{N_{schools}(s)} = \frac{N_{sets}p(s)}{N_{schools}\pi(s)}.$$

Setting the observed counts $n_{schools}$ and n_{sets} equal to their expectation gives

$$n_{schools} \approx E[n_{schools}] = \left(\frac{2Lw_{eff}}{A}\right)N_{schools} \text{ and}$$

$$n_{sets} \approx E[n_{sets}] = f_{trips}N_{sets},$$

where L = the total distance searched by the research vessels;
A = the total area within the stock boundaries; and
f_{trips} = the fraction of tuna vessel trips that carried an observer.

Using the relationship between $\pi(s)$ and $\pi^*(s)$, and these moment equations for $n_{schools}$ and n_{sets}, we estimated the capture frequency for a school of size s as

$$\hat{N}_{capture}(s) = \frac{n_{sets}}{f_{trips}}\frac{2L\hat{w}_{eff}}{An_{schools}}\frac{\hat{p}(s)}{\hat{\pi}^*(s)}.$$

Note that the factor w_{eff} cancels out and only $w_{eff}(s)$ remains.

Because there were so few schools smaller than 100 animals set on by tuna vessels, and so few schools larger than 1000 animals sighted from research vessels, we restricted our analysis to schools from 100 to 1000 animals, and computed estimates of capture frequency at intervals of 100 animals.

Stratification and pooling There were many school size data from tuna vessel sets (n_{sets}=3454), however, there were far fewer research vessel sighting data ($n_{schools}$ = 499) and these had an uneven spatial distribution. We decided that research vessel sightings were too sparse to stratify our estimates of $\pi^*(s)$ and $w_{eff}(s)$ geographically. We did make stratified estimates of $p(s)$, but this had very little effect in absolute terms on the estimates of capture frequency, and so we present only pooled estimates for simplicity.

Similarly, we did not stratify by year in any of our estimates. Set data, trip sampling fractions, sighting data, and search effort were combined to make a single estimate of the average N_{sets} and $N_{schools}$ over all years.

Extrapolation to the international fleet and to annual estimates Data from individual sets came only from U.S. tuna vessels, so that estimating capture frequency due to the entire fleet required extrapolation. We made the assumption that a captain's preference for dolphin school sizes upon which to make sets did not vary with the vessel's country of origin and thus extrapolated our estimate of $p(s)$ to the entire fleet. Our estimates of total numbers of target sets were based on separate observed counts and sampling fractions for the U.S. and the international fleets,

$$\hat{N}_{sets} = \hat{N}_{sets}^{(US)} + \hat{N}_{sets}^{(Intl)} = \frac{n_{sets}^{(US)}}{f_{trips}^{(US)}} + \frac{n_{sets}^{(Intl)}}{f_{trips}^{(Intl)}}.$$

This expression was substituted in for (n_{sets}/f_{trips}) in our estimates of capture frequency for the combined fleet. For non-U.S. vessels, we had only the total number of target sets observed, and we were unable to estimate the variance in $\hat{N}_{sets}^{(Intl)}$. Thus, our estimates for the combined fleet do not include estimates of precision.

Our estimates of capture frequency are strictly valid only for the study period. However, if we assume that the same patterns in school sizes and captain's preference for school sizes hold for the entire year, then the annual capture frequency can be estimated by using the corresponding annual set counts for U.S. and non-U.S. vessels. Because we had only the total number of target sets observed during times other than the study period, our estimates of annual capture frequency do not include estimates of standard error.

Independence of observations

Because of the geographically correlated nature of consecutive research vessel sightings or tuna vessel sets, successive school size observations from a single vessel may not have been independent. This is particularly a concern for the set data, because of the possibility of repeated sets on the same school (see

"Discussion" section). Although dependence does not add a bias to our estimates, it does decrease the effective sample size, which affects our estimates of precision. We accounted for this problem by using bootstrap standard error estimates, and by defining our bootstrap resampling units so as to make them as independent as possible while keeping a reasonably large sample size. For research vessel data, we took days as the resampling unit; for tuna vessels, we resampled by trips. For each bootstrap iteration, we resampled from the research vessel data to achieve approximately the same amount of search effort in each stratum as was actually achieved. We resampled from the tuna vessel data to achieve exactly the actual observed number of trips.

Results

Estimated distribution of school sizes

Figure 2 shows the kernel estimates of the densities $\pi^*(s)$ and $p(s)$. Both estimated densities were much smoother at large school sizes than at small school sizes. This is partially due to the variable bandwidth in the kernel estimator, but primarily due to the data themselves.

Estimated effective strip halfwidth

Figure 3 shows the estimated values for the effective strip halfwidth as a function of school size. Because $\pi^*(s) \propto w_{eff}(s)\pi(s), w_{eff}(s)$ represents the relative amount of "thinning" for schools of different sizes, i.e. $w_{eff}(s)/w$ is the probability of a school of size s being detected from the research vessel, given that it is within the truncation distance w. The estimated values indicate that approximately one third of schools of size 100 within the truncation distance (5.5 km) were missed by the research vessel observers, and essentially all schools of size 1000 were detected. The result shown in Figure 3 is, qualitatively at least, partially constrained by the bivariate line transect model, i.e. if the data indicate dependence of detectability upon school size, then the parametric form for $w_{eff}(s)$ dictates that the estimated curve must vary smoothly and monotonically with size and must approach w asymptotically. However, the model fit need not have any dependence on school size, and the specific direction and rate of increase shown in Figure 3 are due to the data, and agree with observer experience in terms of reaching the limiting value within the range of sizes shown.

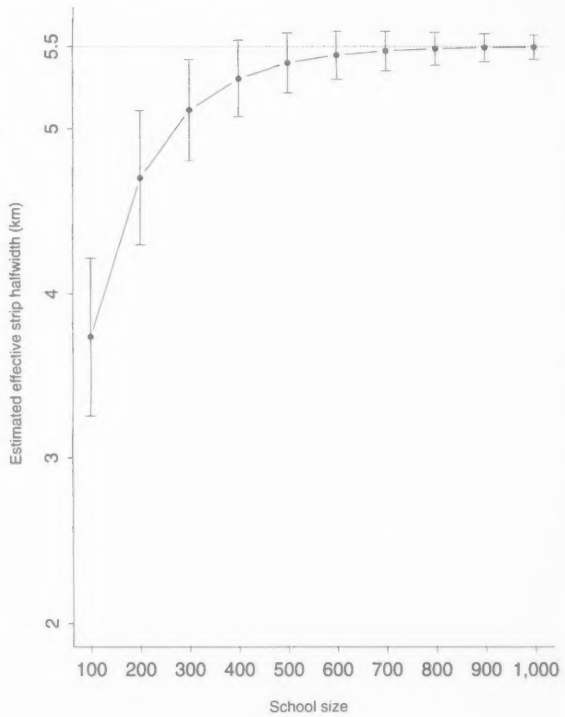


Figure 3

Estimated effective strip halfwidth as a function of dolphin school size. These maximum likelihood estimates are from the bivariate hazard rate line transect model as discussed in the text, and are based on northeastern offshore spotted dolphin school sightings from observers aboard NMFS research vessels during the months July to December, 1986–90 and 1992–92. Error bars indicate plus or minus one standard error and should not be interpreted as confidence intervals. The horizontal line at 5.5 km indicates the perpendicular truncation distance in the line transect model.

The standard error bars in Figure 3 exceed w in some cases, although it is not possible for $w_{eff}(s)$ to exceed the truncation distance w. These error bars are presented simply to represent the estimated precision for each estimate, and should not be interpreted as confidence intervals. Confidence intervals for the estimated halfwidths would tend to be asymmetric and would not exceed the truncation distance.

Estimated capture frequency

Figure 4 shows the estimated capture frequency due to U.S. tuna vessels. These estimates represent the average number of times a school of a given size was set on each year during the study period. The esti-

mates are an integration of the information presented in Figure 2 and Figure 3, i.e.

$$\hat{N}_{capture}(s) \propto \hat{w}_{eff}(s)\hat{p}(s) / \hat{\pi}^*(s),$$

scaled by a suitable estimate of the overall average capture frequency. The magnitude and direction of the trend in $\hat{N}_{capture}$ was almost entirely due to the estimates of $p(s)$ and $\pi^*(s)$. Estimates of the factor $w_{eff}(s)$ varied only by about 50% over the range of sizes considered, whereas the estimated ratio of $p(s)$ to $\pi^*(s)$ varied by two orders of magnitude.

The precisions of our estimates of capture frequency depended on the precisions of the individual estimated factors involved in $\hat{N}_{capture}(s)$. We were able to estimate those different precisions using the output of the bootstrap procedure and found that they varied widely. Much of the variability was in our estimates of $\pi^*(s)$, with bootstrap estimates of CV ranging from 9% at a school size of 100 up to 24% at 1000. Bootstrap CVs for $\hat{w}_{eff}(s)$ were low, ranging from 13% down to 1%, but, as mentioned above, $w_{eff}(s)$ was the factor most constrained by the model. Bootstrap CV's for $\hat{p}(s)$ were lower than those for $\hat{\pi}^*(s)$, ranging from 14% at a school size 100 down to 6% at 1000. Set counts and sighting counts both had bootstrap CV's of approximately 6.5%.

Figure 5 shows the estimated annual capture frequencies due to the U.S. fleet and due to the combined U.S. and international fleet. The estimate of the combined capture frequency for schools of size 1000 is 36.1 sets per year, or one set every 10 days, compared with well under once a year for schools of 100 animals. The estimate for the median school size set on (560 animals) was 10.1 sets per year, or just under once per month. The U.S. fleet accounted for an estimated 31% of sets during the years 1986–90. Although we were not able to estimate standard errors in these annual estimates, the error bars in Figure 4 should give at least a rough idea of the potential precision.

Because of the extrapolation of school-size distributions necessary to make annual and combined fleet estimates, the two curves in Figure 5 are identical in shape to that in Figure 4, but have different scale factors. The scale factor for the lower curve was an estimate of the overall (size-averaged) annual capture frequency, $N_{sets}/N_{schools}$, due to the U.S. fleet, whereas the scale factor for the upper curve was the corresponding estimate for the combined fleets. These two overall capture frequency estimates were not extrapolated from data collected during the study period, but were based on annual set counts for the two fleets.

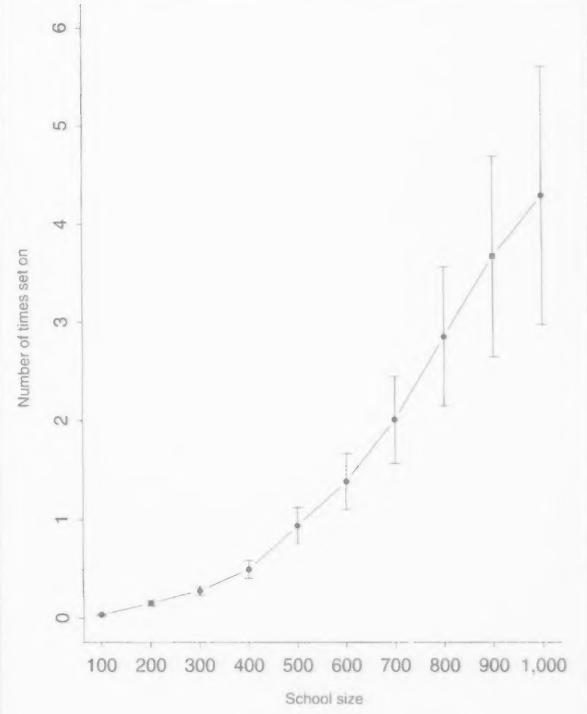


Figure 4

Estimated capture frequency as a function of dolphin school size, for schools of northeastern offshore spotted dolphins. The estimates are of the average number of times a school was set on each year by U.S. tuna purse-seiners, between 28 July and 10 December (19.4 weeks), for the years 1986–90. Error bars indicate plus or minus one standard error and should not be interpreted as confidence intervals.

Using the estimated school sizes from the sighting data, and weighting by the estimated effective strip width, $w_{eff}(s)$, we estimated the cumulative percentage of individual dolphins in schools greater than or equal to a given size, i.e.

$$H(s) \equiv \Pr\{\text{a dolphin is in a school of size} \geq s\}$$

$$= \int_s^\infty t\pi(t)dt \Big/ \int_0^\infty t\pi(t)dt$$

$$\hat{H}(s) = \frac{\sum_i s_i \hat{w}_{eff}(s_i) I\{s_i \geq s\}}{\sum_i s_i \hat{w}_{eff}(s_i)},$$

where $I\{s_i \geq s\} = \begin{cases} 1, & \text{if } s_i \geq s \\ 0, & \text{otherwise} \end{cases}$

and the sums are over research vessel sightings.

Combining $\hat{H}(s)$ with the combined-fleet capture frequency estimates (Fig. 5, upper curve), schools of 1000 animals or greater were estimated to be set on at least once every ten days and contained an estimated 9% of dolphins (Fig. 6). Schools set on most often by tuna purse-seiners, containing from about 250 to 500 dolphins, were estimated to be set on between 2 and 8 times each per year on average; these schools represented just under an estimated one third of the stock. An estimated one half of NE offshore spotted dolphins occurred in schools smaller than 250 animals; schools of this size were estimated to be set on less than twice per year each.

We note that $H(s)$ should not be used to quantify the school size preferences of individual dolphins. For example, although we estimated that schools larger than 1000 animals contained an estimated 9% of dolphins at any given time, this does not imply that the same 9% of dolphins always made up such schools.

Capture frequency for very large schools

Although no kernel estimate of $\pi(s)$ was possible for s greater than 1000 animals, the estimated detection probability for those schools was essentially one out to the truncation distance w, making a rough calculation for capture frequency possible. Because of the rounding tendency of tuna vessel observers, we made an estimate for schools greater than or equal to 1000. With the assumption that the effective strip halfwidth is equal to the truncation distance, an estimate of the average capture frequency due to the entire fleet is

$$\hat{N}_{capture}(s \geq 1000) = \frac{\hat{N}_{sets}^{(large)}}{\hat{N}_{schools}^{(large)}}$$

$$= \frac{n_{sets}^{(US,large)}}{n_{sets}^{(US)}} \left(\frac{n_{sets}^{(US)}}{f_{trips}^{(US)}} + \frac{n_{sets}^{(Intl)}}{f_{trips}^{(Intl)}} \right) \frac{2Lw}{An_{schools}^{(large)}} .$$

The estimated average capture frequency for these very large schools was 51.3 sets per year, or just under once a week.

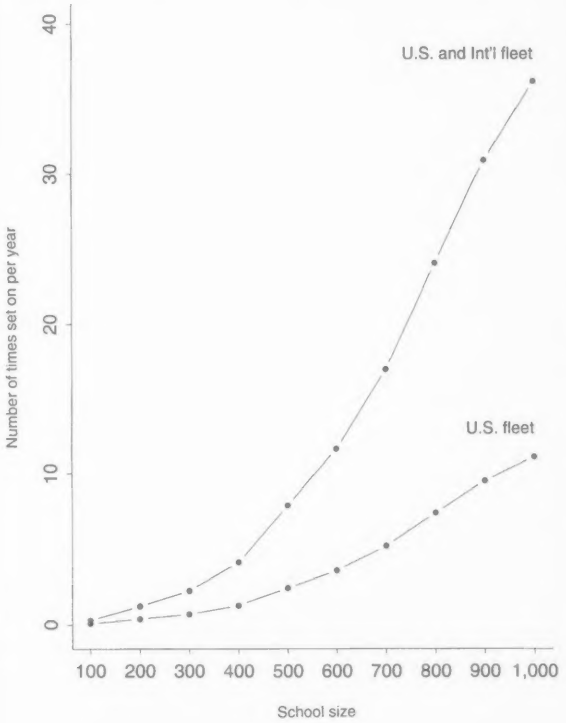


Figure 5

Estimated annual capture frequency as a function of dolphin school size for schools of northeastern offshore spotted dolphins. The estimates are of the average number of times a school was set on each year by tuna vessels in the ETP purse-seine fleet for the years 1986–90. The lower curve shows the number of sets due to U.S. vessels only; the upper curve shows the number of sets due to U.S. and non-U.S. vessels combined. Estimates of standard error were not possible for these estimates.

Discussion

Capture rates for individual dolphins

To interpret these capture frequency results in terms of individual dolphins, we must consider the size range of the schools with which a given individual tends to associate. If one assumes that dolphins have a strong fidelity for a characteristic school size, then the above results indicate that a fixed but relatively small percentage of the dolphin population was consistently subjected to a high rate of capture in purse-seine nets, whereas the majority of dolphins were subject to relatively little disturbance from the fishery. However, little is known about the spatial and temporal dynamics of dolphin schools and their sizes, and a range of other assumptions are possible.

If school membership is completely fluid and dolphins mix perfectly among schools, then over the long term, all dolphins would experience the same capture rate. We made a rough estimate of this rate by estimating the total annual number of dolphins set on and the total number of dolphins. Using data from Table 2, we made a rough estimate of 7610 for the

mean annual number of sets on NE offshore spotted dolphins during the period of this study. From tuna vessel observer data, an estimate for the mean school size for those sets is 773 animals. When combined with an estimate for the total number of NE offshore spotted dolphins (Wade and Gerrodette, 1993), this gives (7610 × 773 dolphins set on) ÷ (731,000 dolphins) = 8.04 sets per dolphin per year.

The true picture certainly lies between these two extremes. On the other hand, if the composition and spatial location of some large schools are static over periods of weeks or longer, then animals in those schools could be subject to short-term capture rates even higher than those of our estimates because of the clustered distribution of fishing effort.

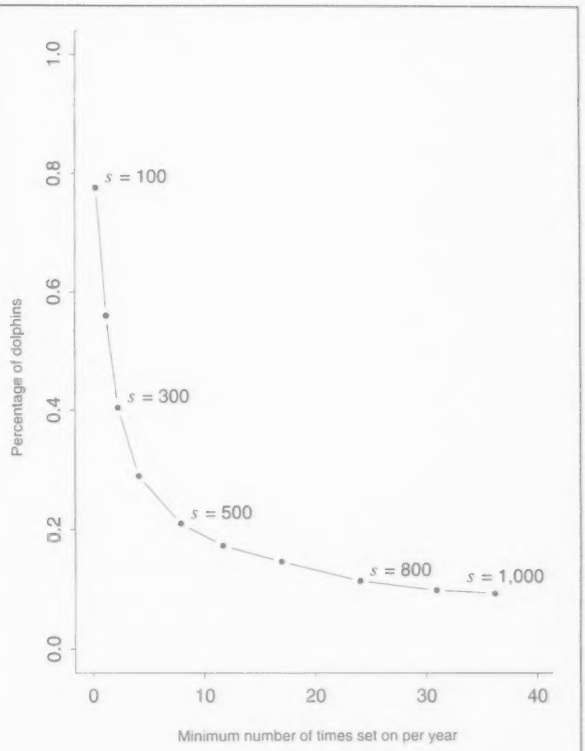


Figure 6

Estimated percentage of northeastern offshore spotted dolphins subject to different levels of capture frequency. The horizontal axis represents the minimum number of times a dolphin school is set upon per year by U.S. and non-U.S. tuna vessels in the ETP purse-seine fleet, for the years 1986-90. The vertical axis represents the estimated fraction of the stock (not the fraction of schools) subject to at least that rate of being set upon. s is the minimum school size accounting for that percentage.

Geographic stratification

Holt et al. (1987) partitioned the ETP into several geographic strata primarily on the basis of spotted dolphin density as observed from tuna vessels during years prior to the study period. In an alternate analysis for capture frequency, we used Holt et al.'s partition to fit separate densities for $p(s)$ in each of two strata (Fig. 1), and used separate counts n_{sets} and $n_{schools}$. The estimates of $p(s)$ from the two strata were significantly different (Kolmogorov-Smirnov goodness-of-fit test, P=0.002), but primarily at smaller school sizes, less than 200 animals, and this stratification made little difference in absolute terms from the unstratified estimates of capture frequency. The similarity in capture frequency estimates between strata indicates that fishing pressure was approximately proportional to dolphin school density.

We did not stratify geographically to estimate $\pi^*(s)$ or $w_{eff}(s)$ because we found that the number of observations in the middle stratum ($n_{schools}$=81) was too small to allow stratification and still have reasonable precision. A Kolmogorov-Smirnov test and Q-Q plots indicated that there was no substantial difference (P=0.62) in $\pi^*(s)$ between strata for the research vessel observers. On the other hand, we fitted the bivariate line transect model to data from the two strata separately and found that the estimate of $w_{eff}(s)$ for the middle stratum was 10–20% smaller than that for the inshore stratum, depending on school size. However, there were few data on which to base either result. One reason why $w_{eff}(s)$ might actually have differed between the two strata was a difference in observed sea state conditions; a higher average Beaufort sea state was reported in the middle stratum. The practical impact is that our estimates of capture frequency may have been overinfluenced by data from the inshore stratum.

Observer size-estimation errors

Our statistical model for the school size data included terms for selection biases, that is, which schools were included in the sighting or set data. However, there was also a potential for observer size-estimation biases. That is, given a sighting of, or a set on, a specific school, an observer had to estimate size of the school. The results presented here treated the observer estimates as exact counts. We did not include an error term for size estimates in either the kernel density estimates of $\pi^*(s)$ and $p(s)$ or the bivariate line transect estimates of $w_{eff}(s)$.

An observer size estimation bias would scale or otherwise deform those estimates of $\pi^*(s)$ or $p(s)$ (or both), depending on whether the bias was proportional to size or was more complex. Even if the observers were unbiased in their individual estimates, estimation variance would still increase both tails in the density estimates. Thus, if research vessel observers and tuna vessel observers consistently made different errors in estimating school sizes, then the trend in our estimates of capture frequency, e.g. Figure 4, could have been in part or entirely due to those errors.

Gerrodette and Perrin[5] studied dolphin school size-estimation errors for research vessel observers by ground-truthing observer estimates against aerial photo counts of the same school. They found that the counts from a single observer could be modeled as lognormally distributed given the true school size. They also found that a given observer in the study might have a substantial positive or negative bias.

Using their photo and observer dataset, we fitted a lognormal model for the geometric means of the observer estimates from each sighting.[6] The fit indicated that the observers had essentially no bias at a true school size near 100, but that there was a negative bias of 21% at a school size of 1000. Because the lognormal is a skewed distribution, this mean bias corresponds to essentially no median bias. The estimated CV for the estimates, given the true size, was 48%.

Given this information, it would have been possible in theory to correct the research vessel observer estimates for bias. However, we did not make that correction because the corresponding correction for the tuna vessel set data was not possible in the absence of a suitable ground-truth study. Significant differences between observers and observing conditions on research vessels and tuna vessels precluded the assumption that any size-estimation biases are similar in the two types of data.

Spatial distribution of schools and school sizes

Our analysis can be taken to imply full spatial mixing, that is, all schools of a given size within the stock boundaries (or within each stratum for the stratified case) have the same probability of being set upon. A more realistic model is that some schools have a higher or lower probability depending not only on their size but also on their geographic location in relation to areas of high school density or high fishing effort. Other factors, such as seasonal effects and the amount of associated tuna, are also interrelated with location in determining the rate of capture for a given school. Because we included only limited spatial information in our model, the appropriate interpretation of our results is that we estimated an average probability of being set upon, as a function of school size, for schools within the stock boundaries (or each stratum).

Observer experience suggests that pressure from fishing on dolphin can reduce average dolphin school size, i.e. areas of high fishing effort tend to have smaller schools.[7] This decrease in school size may be a result of chase and capture operations during sets intentionally or unintentionally splitting schools into smaller subgroups.[8] However, we did not find any indication of such a trend in our NE offshore spotted dolphin school-size data. We concluded that if fishing pressure did affect spotted dolphin school size, its effects may have been masked by size selection in the tuna vessel set data and by the relatively limited number of observations in the research vessel sighting data.

Dolphin schools

Variation in school size over time The simplest interpretation of this analysis would assume that a dolphin school is a fixed entity that does not change in size. If, on the other hand, a school is not a well-defined entity over any length of time, i.e. schools often fragment and reaggregate (e.g., Scott and Cattanach, 1998), then defining capture frequency for anything other than an individual dolphin becomes problematic. The superpopulation model that we used is one way to account for this fluid nature of dolphin schools. In particular, the research and tuna vessel school-size data represent time-averaged samples, i.e., averages over repeated realizations from the superpopulation. Estimated capture frequencies can be interpreted in terms of short-term rates.

Species composition Most schools in both the research vessel and tuna vessel data included not only NE offshore spotted dolphins, but other species as well, primarily spinner dolphins (*Stenella longirostris*). We did not differentiate between pure and

[5] Gerrodette, T. and C. Perrin. 1991. SWFSC Admin. Rep. LJ-91-36, Southwest Fisheries Science Center, La Jolla CA, 74 p.

[6] Details of this exploratory analysis can be found in Perkins, P. C. and E. F. Edwards, 1997, SWFSC Admin. Rep. LJ-97-03, Southwest Fisheries Science Center, La Jolla CA, 36 p

[7] Rasmussen, R. 1997. Southwest Fisheries Science Center, La Jolla, CA. Personal commun.

[8] Hall, M. 1997. Inter-American Tropical Tuna Commission, La Jolla, CA. Some limited data have been collected to study school fragmentation and reaggregation (Perrin et al., 1979; Scott, M. 1997. Inter-American Tropical Tuna Commission, La Jolla, CA. Personal commun.

mixed schools in our analysis. Thus, we took as our population of schools not just those composed purely of NE offshore spotted dolphins, but all schools containing them. School sizes were taken as the total number of animals in each school. This approach would not have been appropriate if we had been estimating a stock-specific abundance (e.g. Wade and Gerrodette, 1993). However, as long as there is no bias in the species composition of schools that are set on, our approach is valid. An exploratory data analysis indicated that the distribution of species proportions was very similar for both research and tuna vessel data.

There was some indication that pure spotted schools tended to be smaller on average than mixed spotted-spinner schools. We did not pursue this because it did not affect our results.

Encounter rate for very large schools

Inspection of Figure 2 raises the question of why so few very large schools (1000 animals or greater) were sighted from the research vessels when so many were set upon by tuna vessels. Only five schools (1% of sightings) in that range were reported by research vessel observers, and the largest was estimated to be 2617 animals. In that range, 896 schools (26% of observed sets) were reported set upon by tuna vessel observers, and 97 were estimated to be larger than 2617 animals. These largest schools from the set data did tend to include slightly higher percentages of species other than spotted dolphins. However, they were still primarily made up of spotted dolphins (just over an estimated 70% on average), and it was not the case that they were due to an association with large groups of, for example, common dolphins (*Delphinus delphis*), which are known to form very large schools (e.g. Edwards and Perrin, 1993).

At least four explanations for this apparent discrepancy are possible. First, this may simply reflect the tuna vessel captains' preference for setting on large schools. Second, the difference may be due to relative bias in size estimation between the two types of observers, as discussed earlier. However, to explain all of the difference, the two sets of observers would have to differ on average by a factor of five in their estimates. Third, the research vessels may have missed a relatively rare segment of the population of schools, which the tuna vessels are able to seek out with a much greater search effort and a nonrandom search strategy. Fourth, some of these large observations in the set data may have been from intentionally repeated sets on the same schools. There is evidence in the tuna vessel observer data for both of these last two explanations, i.e., that localized areas of high density or school size (or both) may exist and that repeated sets on a single school may occur.

Conclusions

The results of this study indicate that tuna purse-seiners in the ETP fishing on NE offshore spotted dolphins have a strong preference for setting on larger than average dolphin schools, and that such schools were subject to being set on at a much higher rate than were smaller schools. Specifically, the largest schools considered, those of 1000 or more animals, were estimated to be set on approximately once every week, whereas the smallest schools considered, those of 100 animals, were estimated set on less than once a year. Our estimated capture rates should be taken as averages for a given school size and do not account for variation due to other factors, such as geographic location or the amount of associated tuna. Also, although we estimated rates in terms of sets per year, we do not assert that the short-term capture rate for a given school is constant, i.e. that sets occur at evenly spaced intervals throughout the year. For example, relatively few sets are made "on dolphin" in the NE offshore stock range during June and July (e.g. Edwards and Perkins, 1998).

These results do not account for any errors in estimation of dolphin school size. Although potential errors in school-size estimates made by research vessel observers were investigated, no corresponding study of potential errors for tuna vessel observer estimates was possible.

To draw conclusions about capture frequency for an individual dolphin, we must consider the size range of the schools with which a given individual tends to associate. Our results imply that dolphins associating primarily with large schools will be subjected to capture much more often than individuals associating primarily with small schools. However, we also estimated that the largest schools are relatively rare and account for a minority of the total number of individual dolphins at any given time. These results may imply that a fixed but relatively small percentage of the dolphin population was consistently subjected to a high rate of capture in purse-seine nets but that a majority of dolphins occur in schools smaller than those apparently preferred by purse-seiners, and experience relatively few captures per year.

However, little is known about the spatial and temporal dynamics of dolphin schools and their sizes, and other conclusions are possible. If dolphins associate with a wide range of school sizes, then the capture rates for individual dolphins would tend to "av-

erage out" and thus would vary less than the range of capture rates for schools. On the other hand, differences between schools in factors other than size could lead to short-term individual capture rates that are even higher than our estimates.

Acknowledgments

We thank M. Hall, M. Garcia, C. Lennert, and M. Scott of the Inter-American Tropical Tuna Commission, and W. Armstrong, J. Barlow, R. Holt, A. Jackson, R. Rasmussen, and K. Wallace of the SWFSC, for the benefit of their field experience and their technical knowledge of the tuna vessel observer program, the NMFS research cruises, and the related databases. Special thanks to T. Gerrodette of the SWFSC and D. Palka of the NEFSC for theoretical and practical advice on the bivariate hazard rate model. We also thank J. Barlow, B. Curry, T. Gerrodette, M. Hall, P. Kleiber, and two anonymous reviewers for their comments on draft versions. Finally, we gratefully acknowledge all of the scientists, observers, NOAA officers and crew, and fishermen who participated in the collection of the research vessel observer data and the tuna vessel observer data.

Literature cited

Burnham, K. P., D. R. Anderson, and J. L. Laake.
1980. Estimation of density from line transect sampling of biological populations. Wildlife Monograph 72, supplement to Journal of Wildlife Management 44, 202 p.

Dizon, A. E., W. F. Perrin, and P. A. Akin.
1992. Stocks of dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific: a phylogeographic classification. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 119, 20 p.

Drummer, T. D., and L. L. McDonald.
1987. Size bias in line transect sampling. Biometrics 43:13–21.

Edwards, E. F., and P. C. Perkins.
1998. Estimated tuna discard from dolphin, school, and log sets in the eastern tropical Pacific Ocean, 1989–92. Fish. Bull. 96:210–222.

Edwards, E. F., and C. Perrin.
1993. Effects of dolphin group type, percent coverage, and fleet size on estimates of annual dolphin mortality derived from 1987 U.S. tuna-vessel observer data. Fish. Bull. 91:628–640.

Hill, P. S., R. C. Rasmussen, and T. Gerrodette.
1991. Report of a marine mammal survey of the eastern tropical Pacific aboard the research vessel *David Starr Jordan*, July 28–December 6, 1990. U.S. Dep. Commer., NOAA Tech. Memo. NMFS NOAA-TM-NMFS-SWFSC-158, Southwest Fisheries Science Center, La Jolla, CA, 133 p.

Holt, R. S., T. Gerrodette, and J. B. Cologne.
1987. Research vessel survey design for monitoring dolphin abundance in the eastern tropical Pacific. Fish. Bull. 85:435–446.

IATTC (Inter-American Tropical Tuna Commission).
1989. Incidental mortality of dolphins in the eastern tropical Pacific tuna fishery, 1979–1988: a decade of the Inter-American Tropical Tuna Commission's scientific technician program. Working document 2 from the tuna-dolphin workshop held 14–16 March, 1989 in San Jose, Costa Rica. Inter-American Tropical Tuna Commission, La Jolla, CA, 90 p.
1991. Tuna-dolphin program field manual. Inter-American Tropical Tuna Commission, La Jolla, CA, 170 p.

Jackson, A. R.
1993. Summary of 1989 U.S. tuna-dolphin observer data. U.S. Dep. Commer., NOAA Tech. Memo. NMFS NOAA-TM-NMFS-SWFSC-183, Southwest Fisheries Science Center, La Jolla, CA, 31 p.

Mangels, K. F. and T. Gerrodette.
1994. Report of cetacean sightings during a marine mammal survey of the eastern topical Pacific on the research vessels *David Starr Jordan* and *MacArthur*, July 28–November 2, 1992. U.S. Dep. Commer., NOAA Tech. Memo. NMFS NOAA-TM-NMFS-SWFSC-200, Southwest Fisheries Science Center, La Jolla, CA, 74 p.

Myrick, A.C., Jr., and P. C. Perkins.
1995. Adrenocortical color darkness and correlates as indicators of continuous acute premortem stress in chased and purse-seine captured male dolphins. Pathophysiology 2:191–204.

NMFS (National Marine Fisheries Service).
1992. Purse seine observer field manual. National Marine Fisheries Service, Long Beach, CA, 258 p.

NCR (National Research Council).
1992. Dolphins and the tuna industry. National Academy Press, Washington D.C., 176 p.

Orbach, M. K.
1977. Hunters, seamen, and entrepreneurs: the tuna seinermen of San Diego. Univ. California Press, Berkeley, CA, 304 p.

Palka, D. L.
1993. Estimating density of animals when assumptions of line-transect surveys are violated. Unpublished Ph.D. diss., Univ. California, San Diego, CA, 169 p.

Perrin, W. F., W. E. Evans, and D. B. Holts.
1979. Movements of pelagic dolphins (*Stenella* spp.) in the eastern tropical Pacific as indicated by results of tagging, with summary of tagging operations, 1969–76. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-737, 14 p.

Scott, M. D., and K. L. Cattanach.
1998. Diel patterns in aggregations of pelagic dolphins and tunas in the eastern Pacific. Mar. Mamm. Sci. 14:401–428.

Silverman, B. W.
1986. Density estimation for statistics and data analysis. Chapman and Hall, London, 175 p.

Wade, P. R., and T. Gerrodette.
1993. Estimates of cetacean abundance and distribution in the eastern tropical Pacific. Rep. Int. Whal. Comm. 43:477–493.

Regional and temporal variability in growth and mortality of bay anchovy, *Anchoa mitchilli*, larvae in Chesapeake Bay

Gene C. Rilling

Edward D. Houde

University of Maryland Center for Environmental Science
Chesapeake Biological Laboratory
P.O. Box 38
Solomons, Maryland 20688-0038
Present address (for G. C. Rilling): Connecticut Department of Environmental Protection
Office of Long Island Sound Programs
79 Elm Street, Hartford, Connecticut 06106-5127;
E-mail address (for G. C. Rilling): chris.rilling@po.state.ct.us

Abstract.—Temporal and spatial variability in growth and mortality rates of bay anchovy, *Anchoa mitchilli*, larvae was analyzed in Chesapeake Bay. Larvae were collected in cruises during June and July 1993, on transects spaced at 18.5-km (10 nmi) intervals over the entire bay. Growth and mortality rates were estimated in lower, mid, and upper bay regions and analyzed in relation to environmental variables, predators (biovolumes of the scyphomedusa *Chrysaora quinquecirrha* and the ctenophore *Mnemiopsis leidyi*), and larval prey (zooplankton abundances). Otolith increment analysis indicated that the mean baywide growth rate of larvae increased significantly from 0.59 mm/d in June to 0.72 mm/d in July. The baywide mortality rate of larvae declined from 0.41 (33.6%/d) in June to 0.23 (20.5%/d) in July. In each month, regional mortality rates were highest in the lower bay. Regionally, mortality ranged from a low of 0.14 (13.1%/d) in the upper bay in July to a high of 0.54 (41.7%/d) in the lower bay in June. Mortality rates declined with increasing larval size. Stage-specific survival was both size-specific and growth-rate dependent as indicated by trends in mortality (M), weight-specific growth (G), and the M/G ratio. Growth rates were positively correlated with temperature and zooplankton abundance. Larval abundances, but not mortality rates, were negatively correlated with gelatinous predator biovolumes. Recruitment potential of bay anchovy was judged to be highest in July in the lower third of Chesapeake Bay. Although lower, production of anchovy prerecruits in June and in other Bay regions was substantial and contributed significantly to prerecruit abundances in 1993.

Manuscript accepted 13 July 1998.
Fish. Bull. 97:555–569 (1999).

In highly fecund fishes that spawn serially over a protracted season and a broad geographic range, variable patterns of cohort successes and failures may result that not only lead to fluctuating recruitments but that are difficult to detect in the absence of sampling programs that are temporally and spatially intensive. We estimated temporal and regional variability in larval-stage growth and mortality of bay anchovy (*Anchoa mitchilli*), an abundant (Hildebrand and Schroeder, 1928) and highly productive species (Newberger and Houde, 1995; Wang and Houde, 1995) in Chesapeake Bay. In exploratory analyses and simulations, Houde (1996, 1997b) demonstrated that variability in recruitment success of bay anchovy can occur when stage-specific mortality rates vary during early life. Recently, individual-based models of bay anchovy dynamics in Chesapeake Bay have demonstrated how stage-specific mortality and growth processes may operate and how density-dependent regulation could dampen fluctuations in abundance (Wang et al., 1997).

Bay anchovy are an important component of the Chesapeake Bay food web. They are not commercially exploited but are a major prey of harvested species such as bluefish (*Pomatomus saltatrix*), weakfish (*Cynoscion regalis*), and striped bass (*Morone saxatilis*) (Hartman and Brandt, 1995) and may represent up to 90% of piscivorous fish diets seasonally (Baird and Ulanowicz, 1989). Spawning by bay anchovy is widespread in the Bay and occurs over a broad range of temperatures and salinities (Dovel, 1971; Houde and Zastrow, 1991). Bay anchovy is a pelagic, serial spawner (Luo and Musick, 1991; Zastrow et al., 1991) that spawns most intensively from May through August in Chesapeake Bay, where it may account for 96–99% of fish egg and 67–88% of larval catches (Olney, 1983). During peak spawning, densities of eggs frequently range from 10 to >1000/m^3 and densities of larvae from 1 to >100/m^3 (Olney, 1983; Dalton, 1987; Dorsey et al., 1996; MacGregor and Houde, 1996; Rilling and Houde, manuscript in review). Within a spawning season, regions of highest egg and larval abundances may shift, as they did from the upper to the lower bay between June and July 1993 (Rilling and Houde, manuscript in review). Such shifts may have important repercussions for bay anchovy production and for production of other fish species and inverte-

brate predators that rely upon bay anchovy as prey.

Because bay anchovy eggs and larvae, and its gelatinous predators, peak in abundance during summer, temporally and spatially variable predation is potentially a significant factor controlling bay anchovy survival and recruitment. Results of mesocosm experiments (Cowan and Houde, 1993) have indicated that up to 20–40% of bay anchovy eggs and larvae in Chesapeake Bay during the peak spawning season may be consumed daily by jellyfish. Purcell et al. (1994) analyzed jellyfish gut contents and estimated that these predators could account for up to 21% of the daily egg mortality and 41% of the larval mortality of bay anchovy in Chesapeake Bay. In site-specific studies, Dorsey et al. (1996) estimated that jellyfish accounted for 0–35%/d of egg mortality, and from 0 to 15%/d of yolksac larval mortality.

Minor variability in daily mortality or growth rates in a 30–50 d period during early life, can generate tenfold or greater differences in recruitment potential of marine fish (Cushing, 1975; Houde, 1987, 1989b). Previous studies in Chesapeake Bay have documented variability in anchovy egg and larval abundances and yolksac larval dynamics at regional scales (Dorsey et al., 1996; MacGregor and Houde, 1996), but this study is the first to provide a comprehensive overview of larval dynamics for the entire Chesapeake Bay. At the outset, we proposed that there are regional and temporal differences or patterns in growth and mortality rates of bay anchovy larvae in Chesapeake Bay. To test this hypothesis, we analyzed otolith microstructure to estimate and compare month-specific (June vs. July), and region-specific (three regions) growth and mortality rates. Increments are deposited daily on sagittal otoliths of bay anchovy, providing a record of age (Fives et al., 1986; Leak and Houde, 1987; Castro and Cowen, 1991; Zastrow et al., 1991). Deposition of otolith increments begins on the third day after hatching and has been documented in laboratory experiments (Leak and Houde, 1987). Here, we discuss how regional or temporal variability in growth and mortality might influence potential for recruitment and production. We compared growth and mortality rates of bay anchovy larvae in relation to abundances of gelatinous predators and zooplankton (larval prey), and in relation to salinity and temperature. Overall, our objective was to determine which region(s) of the Bay and what part of the spawning season contributed most to survival and subsequent production of bay anchovy early-life stages.

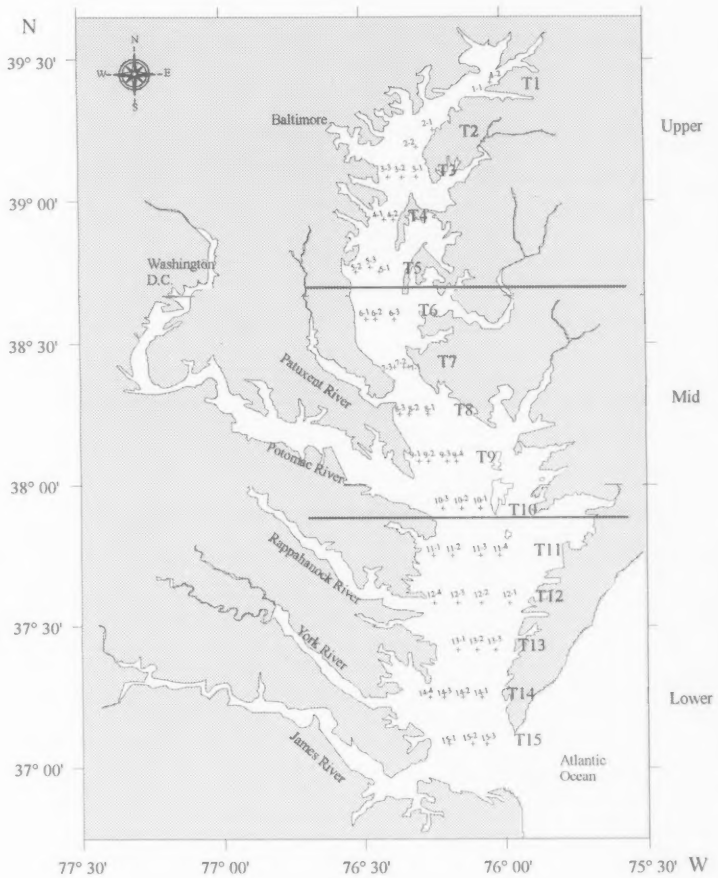


Figure 1

Chesapeake Bay. Regions, transects, and station locations for ichthyoplankton samples, zooplankton samples, and CTD casts, 19–22 June and 23–30 July 1993.

Materials and methods

Ichthyoplankton was collected throughout Chesapeake Bay during two baywide cruises, 19–22 June and 23–30 July 1993 (Fig. 1). Forty-six stations were sampled in June and 48 in July. Stations were on 15 transects spaced at 18.5-km (10 nmi) intervals from

the head of the Bay (39°25'N) to near the Bay mouth (37°05'N). Data were analyzed and compared in three regions: upper bay—transects 1–5 (39°25'N–38°45'N); mid bay—transects 6–10 (38°45'N–37°55'N); and lower bay—transects 11–15 (37°55'N–37°05'N).

At each station, ichthyoplankton was collected in one net of an opening-closing, 60-cm bongo sampler with 280-µm meshes and preserved in ethanol. Two tows, of 2-min duration, were made at each station. The first tow was from within 1 m of bottom to the pycnocline, and the second was made from the pycnocline (or middepth when no pycnocline was present) to the surface. Sampling protocols and methods to estimate densities and abundances of organisms are detailed by Rilling and Houde, manuscript in review); only brief descriptions are given here.

Immediately before each tow, a conductivity-temperature-depth (CTD) cast was made from within 1.0 m of bottom to within 1.0 m of the surface to provide depth profiles of temperature, salinity, and dissolved oxygen. To make results comparable to those of Dorsey et al. (1996) and MacGregor and Houde (1996), temperature, salinity, and dissolved oxygen were examined at 3-m depth. Zooplankton from either three or four designated depths was sampled in 10-L Niskin bottles and collected on 35-µm mesh. Gelatinous zooplankters from each ichthyoplankton tow were counted and their biovolumes recorded.

In the laboratory, anchovy larvae were measured to the nearest 0.1 mm standard length (SL). Lengths were corrected for shrinkage during collection and preservation (Theilacker, 1980; Leak, 1986). Small larvae of bay anchovy may be extruded through net meshes (Leak and Houde, 1987). Therefore, we applied a regression method to adjust abundances of <5.5 mm SL larvae collected in the 280-µm net meshes. The regression, which adjusted abundances of larvae upward by factors of 2.3 (at 2.0 mm), 1.9 (at 3.0 mm), 1.6 (at 4.0 mm), and 1.2 (at 5.0 mm larvae), was derived from comparisons of length-specific abundances in paired tows of 53-µm and 280-µm mesh bongo nets made in Chesapeake Bay under conditions similar to those during this survey (MacGregor, 1994; Rilling and Houde, manuscript in review).

Otolith analysis

Otolith microstructure was analyzed to estimate age, growth, and mortality. In the present study, sagittal otoliths from 509 larvae were examined. Otoliths from representative samples of larvae from each region of the Bay were examined for each cruise. Each larva in the otolith analysis was measured to the nearest 0.1 mm SL. Otoliths from larvae of 2.0 to 25.0 mm SL were mounted in "Epon" under a cover slip, and heated for 24 h at 60°C to harden the epoxy (Secor et al., 1991). Otolith increments were counted on two separate occasions under a compound light microscope at 600 to 1000× magnification by one reader (Rilling). The mean of the two increment counts plus two days was the estimated age.

Growth rates

Growth in length of larvae (mm/d) was estimated from the slopes of the linear regressions of shrinkage-adjusted lengths (SL) on ages from daily otolith-increment analysis:

$$L_t = a + gt,$$

where L_t = standard length (mm) at age t (d);
t = age (d) = otolith increment count plus two days;
g = growth rate (mm/d); and
a = y-intercept, the estimated length (mm) SL at hatch.

Gompertz growth models (Bolz and Burns, 1996) also were fitted to the data for each region and cruise. The fits were no better than those for the linear model and were not considered further in our analysis.

Larval lengths were converted to dry weights (g) from a weight-length relationship:

$$W = 0.1550 \times L^{3.5307},$$

where W = dry weight (g); and
L = mm SL.

Rates of growth in weight then were estimated from an exponential model, fitted by regressing $\log_e$-transformed dry weights on age:

$$W_t = W_0 e^{Gt},$$

where W_t = dry weight (g) at age t (d);
W_0 = dry weight (g) at hatch (the y-intercept of the log-linear regression); and
G = weight-specific growth coefficient (/d).

Coefficients in growth-model regressions were compared among regions and between cruises (months) in analysis of covariance (ANCOVA). The ANCOVAs tested for differences in slopes (growth rates) and y-intercepts in the growth equations. When significant differences were found, a multiple range test (Student-Newman-Keuls) was applied to determine which of the growth rates differed significantly. The

mean baywide growth-in-length and growth-in-weight rates for each cruise were estimated from regressions fitted to pooled length and age data from all stations. Because larvae collected in June were ≤13 mm SL, growth rates of larvae collected in July were estimated from two separate regressions—one for larvae ≤13 mm SL that was directly comparable to the June data and one for larvae >13 mm SL.

Mortality rates

Age-length keys were developed to convert larval length distributions to age distributions from which mortality rates then were estimated. To derive the keys, linear regressions, based upon subsamples of otolith-aged larvae from each cruise and region, were fitted to larval age-on-length relationships. For each regression, the standard error of the estimated regression coefficient was used to calculate a standard normal deviate (z-statistic) from which probabilities of ages of larvae within 1.0-mm length classes were obtained. Six age-length keys were constructed, one for each region and cruise. This maintained the region-specific integrity of size-at-age data, allowing estimation of region-specific mortality rates.

Instantaneous daily mortality rates of larvae were estimated from an exponential model of decline in abundance with respect to age:

$$N_t = N_0 e^{-Mt},$$

where N_t = abundance (number/m^2) at age t (d);
N_0 = estimated initial abundance (y-intercept of regression; number/m^2);
M = instantaneous mortality coefficient (/d); and
t = age (d).

The data were fitted to the log-linear form of the model after $\log_e$-transformation of the abundance data.

Region-specific mortality coefficients were estimated and compared within each cruise by analysis of covariance (ANCOVA). Mean baywide mortality rates for each cruise (month) were estimated by pooling abundance-at-age data from all stations and then compared in ANCOVA. When significant, ANCOVAs were followed by a multiple comparison test (Student-Newman-Keuls) to determine which mortality estimates differed significantly. Two separate mortality rates were estimated for larvae collected in July—one for larvae ≤13 mm SL (<18-day-old larvae) that was directly comparable to the June data that included only larvae of those ages, and one for larvae >13 mm SL (≥18-day-old larvae). Length-specific mortality rates also were estimated, by regressing $\log_e$-transformed abundances of larvae on 1-mm length classes.

M/G ratio and stage-specific survivorship

Stage-specific survival can be estimated from the M/G ratio, where M is the instantaneous mortality rate, and G is the weight-specific growth coefficient. The M/G ratios were compared between cruises and among the three designated regions of Chesapeake Bay. The ratio M/G is an indicator of stage-specific survivorship and production potential of larval cohorts (Houde, 1996, 1997a, 1997b). The ratio, sometimes termed the "physiological mortality rate," expresses a population's mortality per unit of individual growth (Beyer, 1989).

Stage-specific survival of bay anchovy larval cohorts was estimated as

$$S = [W_s / W_0]^{-(M/G)},$$

where S = stage-specific survival = N_s/N_0;
N_s = number of survivors at the end of a stage;
N_0 = number alive at the beginning of a stage;
W_s = dry weight of a 12-mm-SL bay anchovy larva (1000 mg);
W_0 = dry weight of a 3-mm-SL bay anchovy larva (10 g). [Note: This weight is more accurate than weight estimated for a 3-mm larva from the weight-length relationship, which overestimated weights of the smallest larvae]; and
M/G = ratio of instantaneous mortality coefficient (M) and weight-specific growth coefficient (G).

Survival to 12 mm SL, the largest length class fully represented in collections in each of the months, was calculated for each region by multiplying stage-specific survival rate (S) by estimated abundance of the smallest fully represented length class (i.e. N_0 at 3 mm SL). Stage-specific survival rates also were estimated for egg to 3-day larva, 3-day to 10-day larva, and 10-day to 18-day larva. Age-specific production at a station was obtained by multiplying estimated larval density (number/m^3) by the volume represented by the station. Regional productions were obtained by summation of larval abundances for all stations in each region.

Correlations and predictions

Multiple regression analyses were applied to determine if bay anchovy larval growth and mortality

rates could be related to biological or environmental factors. The four independent variables considered for inclusion were gelatinous predator biovolume (mL/m^2), zooplankton density (number/L), temperature, and salinity. Mean regional estimates of independent variables were entered into the regression model. Prior to multiple regression analysis, simple correlation analyses were run to determine which independent variables might be colinear and unsuitable for inclusion in the multiple regression model (SAS Institute, 1990). Pairs of independent variables with a correlation coefficient >0.70 were considered highly correlated and thus excluded from the multiple regression analysis.

Zooplankton analyses

In the laboratory, zooplankton organisms were identified by using a dissecting microscope. Zooplankton that were potential prey of larval anchovy were enumerated, i.e. copepods, barnacle nauplii, gastropod veligers, bivalve veligers, cladocerans, rotifers, tintinnids, polychaete larvae, and chaetognaths. Copepods were categorized as adults, copepodites, and nauplii. Densities of zooplankters were calculated as

$$D = N/V,$$

where D = density of organisms (number per liter);
N = number of organisms in a 10-L Niskin-bottle sample; and
V = sample volume (10 liters).

Densities were weighted according to the depth range represented by each sample to obtain a weighted mean density in the entire water column:

$$\overline{D} = \frac{\sum_{i=1}^{k} D \times m}{\sum_{i=1}^{k} m},$$

where m = depth ranges represented by each Niskin-bottle sample; and
k = number of Niskin-bottle samples taken on a CTD cast (3 or 4).

Results

Hydrography

Mean temperatures, salinities, and oxygen levels at 3-m depth in Chesapeake Bay differed significantly between June and July 1993 (t-test, $P<0.0001$). In each month, there was a well established pycnocline. Baywide mean temperature increased from 25.3°C in June to 26.6°C in July. Mean salinity baywide increased from 10.1 psu in June to 15.9 psu in July (Table 1) and increased in both months between the upper and lower regions of the Bay (ANOVA, $P<0.001$). Mean dissolved oxygen levels decreased from 7.8 mg/L in June to 6.3 mg/L in July. In June, 3-m DO levels ranged from 4.1 to 12.6 mg/L ; in July they were lower, 4.6 to 8.4 mg/L. Hypoxic and near-anoxic conditions (≤2.0 mg O_2/L) were most prevalent in the deep channel of the mid bay region, especially in July.

Growth

Baywide, mean growth rate of anchovy larvae increased from 0.59 mm/d in June to 0.72 mm/d in July (ANCOVA, $P<0.001$) (Fig. 2). When the analysis included only larvae ≤13 mm SL, an even higher baywide growth rate was estimated in July (0.78 mm/d) than in June (0.59 mm/d) (ANCOVA, $P<0.001$). Estimated lengths at 15 days after hatching were 11.65 mm SL in June and 13.72 mm SL in July.

Growth rates did not differ significantly among regions in June or July (ANCOVA, $P>0.05$) (Fig. 3). The regional estimates of growth-in-length rates ranged from 0.53 mm/d in the lower bay during June to 0.78 mm/d in the upper bay in July. Although not significantly different, the highest regional growth rates for each month were in the upper bay. The

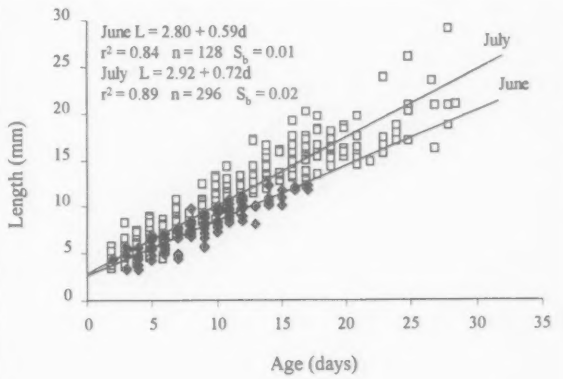


Figure 2

Baywide linear growth models for bay anchovy larvae in Chesapeake Bay, June and July 1993. L = standard length (mm), d = age in days, estimated from otolith-increment analysis. ◆ = June, ▫ = July.

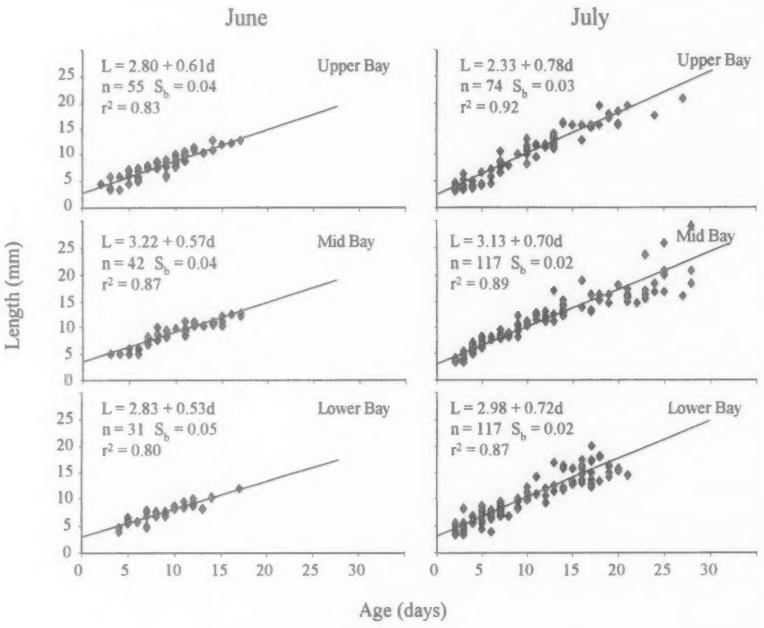


Figure 3

Linear growth models for bay anchovy larvae in upper, mid, and lower Chesapeake Bay regions, June and July 1993. L = standard length (mm), d = age in days, estimated from otolith-increment analysis.

y-intercepts of the linear regressions ranged from 2.33 mm to 3.22 mm and did not differ significantly among regions or between June and July (ANCOVA, $P>0.05$).

Growth in weight was rapid for surviving larvae. Baywide, estimated weight-specific growth rates G (/d) for larvae ≤13 mm SL (Table 1) increased from 0.26 in June (29.7%/d) to 0.35 in July (41.9%/d) (ANCOVA, $P<0.05$). For the ≤13 mm larvae, the highest regional G was 0.40 in the upper bay in July (49.2%/d), and the lowest G was 0.25 in the mid bay in June (28.4%/d). In July, an estimated baywide G for larvae >13 mm SL was only 0.11 (11.6%/d), a rate much lower than that of smaller larvae.

Mortality

Larvae experienced high mortality rates. Baywide instantaneous mortality coefficients M (/d) for larvae in all age classes declined significantly from 0.41 (33.6%/d) in June to 0.23 (20.5%/d) in July (ANCOVA, $P<0.0001$) (Fig. 4). When the data analysis included only larvae <18-days old (the oldest age represented in June) estimated July M = 0.22 (19.7%/d), a rate still significantly lower than the June rate (ANCOVA, $P<0.001$).

Larval mortality rates differed significantly among regions in June and July (ANCOVA, $P<0.0001$). Highest mortality rates in each month were in the lower bay. Regional daily rates ranged from 0.14 (13.1%/d) to 0.54 (41.7%/d) (Fig. 5). In June, the mid bay mortality rate was significantly lower than upper and lower bay rates. In July, when all regional mortality rates differed significantly, the lower bay had the highest mortality rate and the upper bay had the lowest rate (Student-Neumann-Keuls test).

Length-specific mortality rates (/mm) declined dramatically as larval length increased (Fig. 6). In June, the length-specific mortality rates ranged from 0.45/mm for 2–5 mm SL larvae to 0.07/mm for 10–13 mm SL larvae. In July, the rates were lower, ranging from 0.33/mm for 2–5 mm SL larvae to 0.05/mm for 10–13 mm SL larvae. The highest regional length-specific rate, 0.64/mm, occurred in the mid bay during July for the 2–5 mm SL class.

M/G ratio, production, and survival

The baywide M/G ratio declined from 1.59 in June to 0.67 in July (Fig. 7), indicating a nearly 70-fold higher survival and biomass production of cohorts

Table 1

Summarized data, Chesapeake Bay cruises, 19–22 June and 23–30 July 1993. Data include anchovy weight-specific growth rates (/d), mean biovolumes (mL/m^2) of gelatinous predators *Mnemiopsis leidyi* and *Chrysaora quinquecirrha*, mean densities (organisms/L) of zooplankton (ZOOP), mean regional temperatures (T) and salinities (S) at 3-m depth. Identical superscripts indicate no significant difference (P>0.05, Tukey's multiple range test) among regions or between months. SE = standard error.

Region	T (°C)	S (psu)	ZOOP (/L)	Vol. of *M. leidyi* (mL/m^2)	Vol. of *C. quinquecirrha* (mL/m^2)	Weight-specific growth rate G (/d)
June						
Upper bay	25.4^a	5.8^a	326.8^a	41.4^a	0.0^a	0.28^a
SE			116.7	22.1	—	0.01
Mid bay	25.3^a	9.7^b	23.1^b	999.5^b	0.0^a	0.25^a
SE			7.2	211.3	—	0.01
Lower bay	25.3^a	14.7c	68.6^b	516.8^a	0.0^a	0.25^a
SE			21.7	134.4	—	0.02
July						
Upper bay	26.8^a	8.9^a	442.5^a	229.6^a	30.7^a	0.40^a
SE			91.3	65.2	12.1	0.02
Mid bay	26.8^a	12.6^b	162.5^b	204.5^a	36.4^a	0.37^a
SE			35.5	44.7	7.9	0.03
Lower bay	26.2^a	26.2c	277.2^a	12.1^b	22.0^a	0.28^a
SE			40.0	7.2	11.8	0.02
Baywide						
June	25.3^a	10.1^a	138.5^a	560.7^a	0.0^a	0.26^a
SE			43.9	104.2	—	0.01
July	26.6^b	15.9^b	289.0^b	139.1^b	29.5^b	0.35^b
SE				27.4	6.1	

in the 3–12 mm SL size range during July. The increase in growth and decline in mortality rates between June and July accounted for the drops in M/G ratio. On average, larval cohorts lost biomass in June (M/G>1.0), but gained biomass in July (M/G <1.0). In June, cohorts at 12 mm SL supported only 6.6% of the biomass present at 3 mm SL, whereas, in July, cohorts at 12 mm SL supported 457.1% of their 3-mm-SL biomass. Each regional M/G ratio also declined between June and July.

Predicted abundance of larval daily cohorts at 12 mm SL, based upon the M/G ratios and estimated regional abundance-at-age data, was highest in the upper bay in June but shifted to the mid and lower bay in July (Table 2). Stage-specific mortality rates, estimated from declines in abundances, were highest for the youngest stages, and declined with increasing age (Table 3). In this analysis, abundances were estimated for cohorts at 18 days after hatching, when regional mean lengths ranged from 12.4 to 16.4 mm SL. Despite highest regional mortality, daily cohorts from the lower bay in July produced the most 18-day-old larvae (1.5×10^8). The daily production of 18-day-old larvae in the lower bay was 3.4–4.6 times higher than in other regions in July, and from 7 to 50 times higher than in other regions in June.

Cumulative mortalities from egg to 18-day old larval stage were lowest in the mid bay in June but lowest in the upper bay in July. Interestingly, those regions had experienced the greatest egg to 3-day-old larval mortalities, which then were followed by low mortality in older larvae (Table 3).

Predators and prey

There was a significant between-cruises difference in mean combined biovolumes of two common gelatinous predators of bay anchovy eggs and larvae, the ctenophore *Mnemiopsis leidyi*, and the scyphomedusa *Chrysaora quinquecirrha*, (t-test, P<0.001) (Table 1). Mean biovolumes of the ctenophore shifted regionally and declined by a factor of four in July. The scyphomedusan did not occur in June and had a mean biovolume of 29.5 mL/m^2 in July, and there was no indication of regional differences (ANOVA P>0.05) (Table 1).

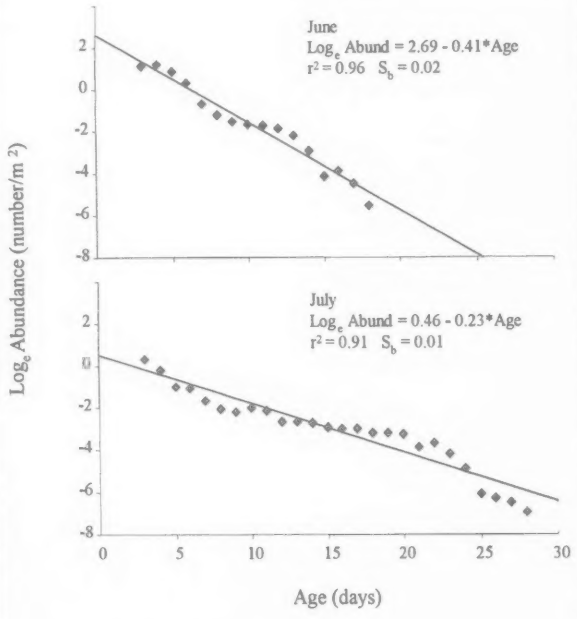


Figure 4

Age-specific survival curves for bay anchovy larvae in Chesapeake Bay, June and July 1993. The age-specific abundance estimates for each day class were derived from age-length keys.

Table 2

Predicted cohort survivorships of bay anchovy larvae in the upper, mid, and lower Chesapeake Bay in June and July 1993. N_0 = estimated number of smallest fully represented length class of larvae (3 mm SL). M/G = ratio of instantaneous mortality rate (/d) to weight- specific growth rate (/d), survival rate (S) = $[W_s/W_0]^{-(M/G)}$ where W_s = dry weight of a 12-mm-SL larva (1000 μg), W_0 = dry weight of a 3-mm-SL larva (10 mg), and apparent survivorship at 12 mm = $S \times N_0$.

Region	N_0 (3-mm-SL larvae)	M/G	Survival rate	Apparent survivorship at 12 mm SL
June				
Upper bay	2.59×10^{10}	1.72	0.0004	1.04×10^{7}
Mid bay	2.49×10^{8}	0.87	0.0180	4.48×10^{6}
Lower bay	7.28×10^{9}	2.17	0.00005	3.64×10^{5}
July				
Upper bay	5.95×10^{8}	0.35	0.200	1.19×10^{8}
Mid bay	2.08×10^{10}	0.62	0.058	1.21×10^{9}
Lower bay	11.72×10^{10}	1.19	0.004	4.69×10^{8}

Baywide, the mean density of zooplankton that are potential prey of anchovy larvae doubled between June and July (t-test, $P<0.05$) (Table 1). Mean density of zooplankton was highest in the upper bay in June (ANOVA, $P<0.05$) and was higher in the upper and lower bay than in the mid bay in July (ANOVA, $P<0.05$). Nauplii of the copepod *Acartia tonsa* were the single most abundant zooplankter collected. Tintinnids, rotifers, and the cyclopoid copepod *Oithona* sp. also were common. Mean density of copepod nauplii, a major prey of bay anchovy larvae, increased from 36.9/L in June to 110.5/L in July (t-test, $P<0.05$).

Correlations

At the regional level, few correlations were judged to be significant at the $\alpha = 0.05$ level between biological and environmental variables (Table 4). The low degrees of freedom ($n=6$) and corresponding low power made it difficult to reject null hypotheses. Several coefficients were high enough to suggest possible correlations. Anchovy larval abundances were positively correlated with egg abundances ($r=+0.96$, $P<0.01$) and negatively correlated with gelatinous predator biovolumes ($r=-0.87$, $P<0.05$) (Fig. 8A). Larval growth rate was positively correlated with temperature ($r=+0.94$, $P<0.01$) (Fig. 8B) and possibly related to zooplankton density ($r=+0.72$, $P<0.11$). Although not significant at $\alpha = 0.05$, anchovy egg abundances and zooplankton densities both may have been negatively correlated with gelatinous predator biovolumes ($r=-0.76$, $P=0.08$).

Predicting larval growth and mortality

Regional variability in anchovy larval growth-in-length rate for the combined June and July cruises was explained reasonably well by a two-variable regression model that included temperature and zooplankton density ($r^2=0.93$):

$$g = 0.32 + 0.05X_1 + 0.004X_2,$$

where g = larval growth rate (mm/d);
X_1 = log$_e$ zooplankton density (organisms/L); and
X_2 = temperature (°C).

Larval growth rates increased with increasing temperatures and zooplankton densities. Temperature accounted for more of the variability in growth rate than did zooplankton density. Observed and model-

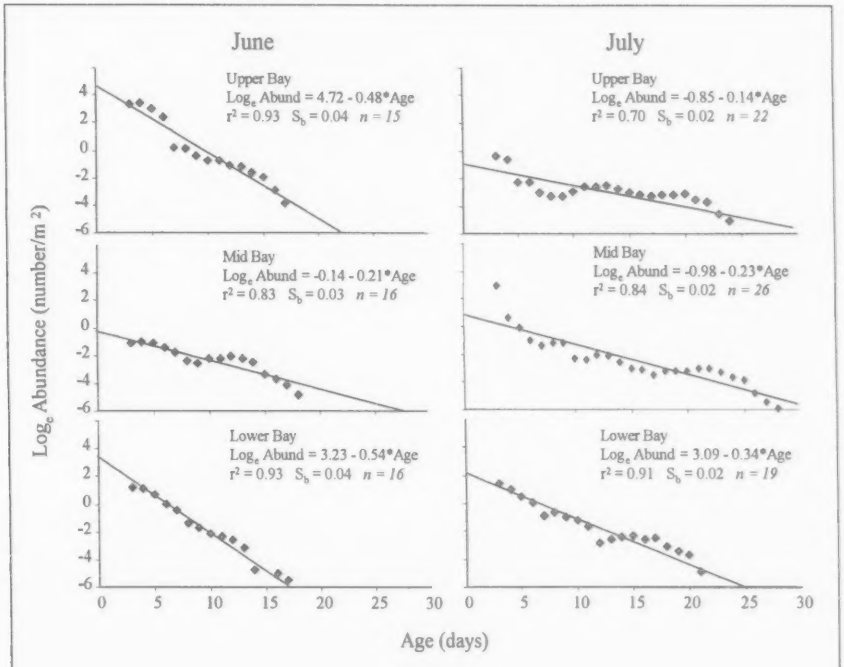

June
July
Upper Bay
Log$_e$ Abund = 4.72 - 0.48*Age
r^2 = 0.93 S_b = 0.04 n = 15
Upper Bay
Log$_e$ Abund = -0.85 - 0.14*Age
r^2 = 0.70 S_b = 0.02 n = 22
Mid Bay
Log$_e$ Abund = -0.14 - 0.21*Age
r^2 = 0.83 S_b = 0.03 n = 16
Mid Bay
Log$_e$ Abund = -0.98 - 0.23*Age
r^2 = 0.84 S_b = 0.02 n = 26
Lower Bay
Log$_e$ Abund = 3.23 - 0.54*Age
r^2 = 0.93 S_b = 0.04 n = 16
Lower Bay
Log$_e$ Abund = 3.09 - 0.34*Age
r^2 = 0.91 S_b = 0.02 n = 19
Log$_e$ Abundance (number/m^2)
Age (days)

Figure 5

Age-specific survival curves for bay anchovy larvae in the upper, mid, and lower Chesapeake Bay regions in June and July 1993. The age-specific abundance estimates for each day class were derived from age-length keys.

Table 3

Estimated abundances, stage-specific mortality rates, and daily cohort production of bay anchovy larvae in the upper, mid, and lower Chesapeake Bay in June and July 1993, based upon declines in total numbers of larvae between stages. Stage A = estimated daily production of anchovy eggs by region. Stage B = estimated number of the smallest fully represented age class of larvae (3-d-old larvae). Stage C = estimated number of 10-day-old larvae. Stage D = estimated number of oldest represented age class of larvae (18-d-old larvae). Apparent loss rates for each stage, and cumulative mortalities also are given.

Region	Stage A (egg production)	Stage B (3-d old larvae)	Apparent loss rate A → B (M/d)	Stage C (10-d old larvae)	Apparent loss rate B → C (M/d)	Stage D (18-d old larvae)	Apparent loss rate C → D (M/d)	Cumulative mortality B → D	Apparent survival
June									
Upper	8.87×10^{11}	2.59×10^{10}	1.18	4.42×10^{8}	0.58	2.16×10^{7}	0.38	7.09	0.0008
Mid	10.44×10^{11}	2.49×10^{8}	2.78	1.06×10^{8}	0.12	6.52×10^{6}	0.35	3.64	0.0263
Lower	23.28×10^{11}	7.28×10^{9}	1.92	1.42×10^{8}	0.56	2.45×10^{6}	0.51	8.00	0.0003
July									
Upper	3.21×10^{11}	5.95×10^{8}	2.09	4.14×10^{7}	0.38	3.26×10^{7}	0.03	2.90	0.055
Mid	1.53×10^{12}	2.08×10^{10}	1.43	1.33×10^{8}	0.72	4.39×10^{7}	0.14	6.16	0.002
Lower	6.58×10^{12}	11.72×10^{10}	1.34	9.29×10^{8}	0.69	1.50×10^{8}	0.22	6.66	0.001

predicted values of mean regional larval growth rates differed by no more than 6%. No satisfactory multiple regression model could be fit for larval mortality.

Discussion

Cohorts of bay anchovy larvae in Chesapeake Bay do not experience uniform growth and mortality.

Growth rates were temporally variable, and mortality rates were both spatially and temporally variable. It was clear that variability in these rates could significantly alter production and recruitment potentials. Baywide, larval growth rates were higher in July than in June. The larval growth rates that we report are higher and more variable than rates reported previously for bay anchovy in the laboratory and in most field studies (Table 5). Gallagher et al. (1983) did report equivalent and higher growth rates (0.59–0.93 mm/d) in the Patuxent River tributary of Chesapeake Bay.

Temporal and spatial variability in anchovy larval growth rates was related to both zooplankton density and temperature. The mean baywide growth rate of larvae increased from 0.59 mm/d in June to 0.72 mm/d in July, corresponding to increases in mean water temperatures and mean copepod nauplii densities. The increase in larval growth rate between months corresponded to a coincident 1.3°C increase in mean temperature at 3-m depth and to a major increase in zooplankton abundance. On the basis of laboratory experiments, Houde (1978) predicted minimal prey concentration for 10% survival of bay anchovy larvae at 26°C to be 107 copepod nau-

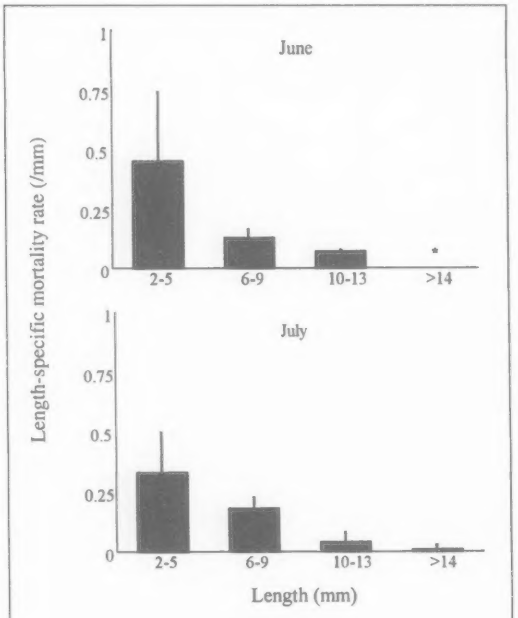


Figure 6

Baywide mean length-specific mortality rates (/mm) of bay anchovy larvae in four length classes during June and July 1993. Error bars are ±1 SE. * = no data.

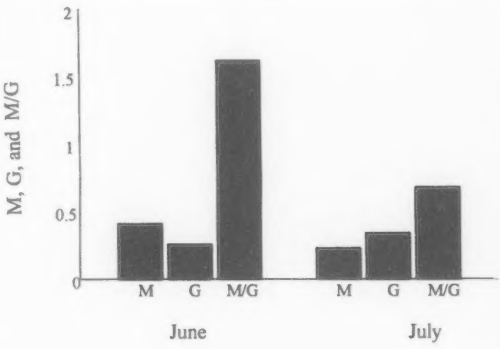


Figure 7

Baywide daily instantaneous mortality rate (M), weight-specific growth rate (G), and M/G ratios for bay anchovy larvae in Chesapeake Bay, June and July 1993.

Table 4

Correlation coefficients at the regional level (n=6) for data collected in Chesapeake Bay, June and July 1993. The seven variables include mean regional instantaneous larval mortality rate (M, /d), larval growth rate (g, mm/d), egg and larval abundances (number/m^2), $\log_e$-combined gelatinous predator biovolumes (mL/m^2) of *Mnemiopsis leidyi* and *Chrysaora quinquecirrha*, zooplankton density (organisms/L), and temperature and salinity at 3-m depth. * = $P<0.05$, ** = $P<0.01$. In each case, $n = 6$, $r_{.05,4} = 0.81$.

	M	g	Egg abundance	Larval abundance	Jelly biovolume	Zooplankton density	Temperature (°C)
g	−0.685						
Egg abundance	0.364	0.056					
Larval abundance	0.434	0.165	0.955**				
Jelly biovolume	−0.287	−0.380	−0.765	−0.868*			
Zooplankton density	−0.039	0.721	0.251	0.477	−0.761		
Temperature	−0.771	0.938**	−0.027	0.037	−0.170	0.555	
Salinity	0.111	0.091	0.524	0.521	−0.132	−0.072	0.067

plii/L. In the present study, nauplii densities often exceeded that level in July, but levels were lower and potentially limiting during June, especially in the mid bay (mean=9.7 nauplii/L) and lower bay (mean=17.7 nauplii/L).

During each month, fastest growth rates were estimated for larvae from the upper bay where copepod nauplii were most abundant (means=84.8 nauplii/L in June and 157.5 nauplii/L in July). Lowest growth was estimated during June in the mid and lower bay, where copepod nauplii densities and mean temperatures were lowest. Although temperature alone may exercise an important control over larval growth, (Houde, 1989a; Pepin, 1991), a combination of factors, including prey availability, effects of body size, or growth-rate dependent mortality, may operate to control growth rates and survival potential (Bailey and Houde, 1989; Heath, 1992; Leggett and DeBlois, 1994). In the case of bay anchovy, all of these factors may operate, but temperature and prey level apparently predominate. There also was an effect of body size; growth rate of larvae >13 mm declined. In a synthesis analysis, Houde (1997b) reported that average weight-specific growth coefficients of bay anchovy declined progressively from 0.573 (77.3%/d) in newly hatched larvae to 0.065 (6.7%/d) in near-metamorphosis individuals.

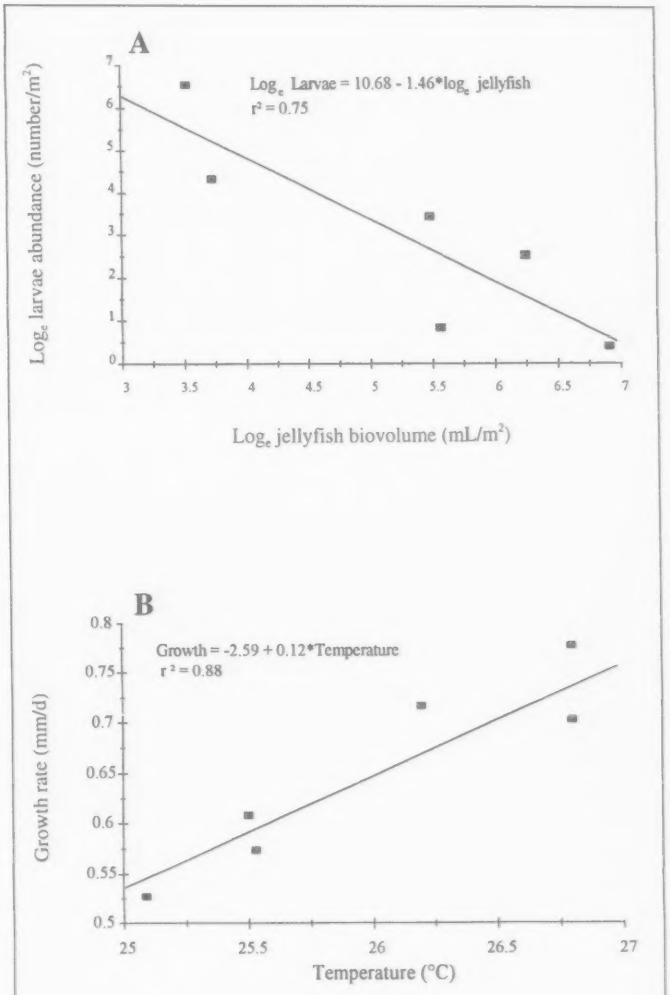


Figure 8

Relationship between (**A**) mean regional bay anchovy larval abundance and gelatinous predator biovolumes and (**B**) mean regional bay anchovy larval growth rates and temperature at 3-m depth in Chesapeake Bay, June and July 1993.

Our baywide instantaneous daily mortality rates decreased from 0.41 in June to 0.23 in July 1993. This decline was coincident with increasing growth rate, suggesting that cohorts of rapidly growing larvae in July might have been less vulnerable to size-selective or growth-rate dependent predation. From length-specific and age-specific analyses of mortality, it was clear that mortality rates were greatest for the smallest and youngest larvae (Table 3). Houde (1997b), analyzed the accumulated data on bay anchovy larvae from Chesapeake Bay and demonstrated that mortality rate (M) declined predictably with respect to body weight raised to the –0.318 power. In the present study, mortality from the egg to 3-day-old larval stage was 2 to 7 times higher than mortality from the 3- to 10-day-old larval stage. Interestingly, mean baywide mortality rates for the egg to 3-day-old stage (yolksac and first-feeding larvae) were similar in June and July (82%/d in June, 79%/d in July), but mortality rates for the 10 to 18-day-old larval stage were considerably lower in July (34%/d in June, 12%/d in July), implying that conditions had become more favorable for feeding-stage larvae in July. Baywide cumulative mortality rates for egg to 18-day-old larvae indicated that <0.1% of a daily cohort survived to 18 days after hatching in June and that ~1.6% survived to 18 days in July.

Predation is a major cause of mortality in the early life of marine fishes (Leggett, 1986; Bailey and Houde, 1989; Leggett and DeBlois, 1994) and may

Table 5

Reported growth and mortality rates of bay anchovy larvae in field studies.

Location	Growth (mm/d)	Mortality (M/d)	Source
Patuxent River, MD	0.59–0.93		Gallagher et al. (1983)
Newport River Estuary, NC	0.25–0.51		Fives et al. (1986)
Biscayne Bay, FL	0.43–0.56	0.30–0.45	Leak and Houde (1987)
Mesocosms in Chesapeake Bay, MD	0.39–0.61	0.08–0.23	Cowan and Houde (1990)
Great South Bay, NY	0.52–0.59	0.32–0.89	Castro and Cowen (1991)
Chesapeake Bay, MD (yolksac larvae)		0.41–4.24	Dorsey et al. (1996)
Chesapeake Bay, MD		0.23–1.20	MacGregor and Houde (1996)
Chesapeake Bay, MD	0.53–0.78	0.14–0.54	This study, range of regional rates

be the major agent of mortality operating on bay anchovy in Chesapeake Bay. The gelatinous zooplankters *M. leidyi* and *C. quinquecirrha,* are known to be important predators on eggs and larvae of bay anchovy (Feigenbaum and Kelly, 1984; Monteleone and Duguay, 1988; Cowan and Houde, 1993; Purcell et al., 1994). In Chesapeake Bay, the peak periods of bay anchovy spawning and gelatinous zooplankton abundance overlap during June and July (Cowan and Houde, 1993; Purcell et al., 1994), facilitating the predator-prey interaction. We found gelatinous predator biovolumes to be significantly higher in June, when only *M. leidyi* was present, than in July when both species occurred. *Chrysaora quinquecirrha*, a potentially more powerful predator on anchovy eggs and larvae than *M. leidyi* (Purcell et al., 1994), occurred only in July, but at low mean biovolumes that were uniform in the three Bay regions. It is worth noting that *C. quinquecirrha* is also a predator on *M. leidyi* (Purcell and Cowan, 1995), resulting in a predator-prey interaction that potentially has a sparing effect on anchovy eggs and larvae (Cowan and Houde, 1992).

The large biovolumes of gelatinous predators probably contributed to the greater mortality rates in June compared with July. However, the six mortality coefficients from the regional estimates were not significantly correlated with gelatinous predator biovolumes (Table 4), despite the strong, negative, linear relationship between anchovy larval abundance and gelatinous predator biovolume (r^2=0.75; Fig. 8A) for the combined June and July regional data. This negative correlation may have been a consequence of predation, but it also could have been generated by lower egg production of anchovy in areas where jellyfish were abundant, as Dorsey et al. (1996) hypothesized in site-specific studies of bay anchovy egg and yolksac larval mortality. Although we cannot conclude unequivocally that gelatinous predators accounted for high mortality rates, it is likely that they were significant consumers of anchovy larvae.

Abundance data illustrated in survival curves (Figs. 4 and 5) showed several modes, which suggested that cohort-specific mortality might be variable on shorter time scales than we studied and might be changing as a function of ontogeny, age, or size. Other factors also could have biased our mortality estimates or contributed to regional variability in rates, for example, pulses of spawning that produce variable initial abundances of daily cohorts or immigration and emigration of larvae into and out of a region. Because mortality is size-specific, the presence of larger larvae in July could have led to a lower estimate of mortality rate during that period. But, when only larvae of equivalent lengths (i.e. ≤13 mm SL) were analyzed, estimated mortality rates remained nearly twice as high in June (M=0.41) as in July (M=0.22). If some larvae were being advected up the bay, as Dovel (1971) had hypothesized, this process could have contributed to biased estimates of higher mortality rates in the lower bay.

Despite a high cumulative mortality rate, the lower bay in July had the highest production of larvae surviving to 18 days after hatching for the June–July 1993 period (Table 3). This result is due to high spawning activity and initial concentrations of larvae in the lower bay (Rilling and Houde, manuscript in review), a high growth rate of larvae, and, importantly, the relatively large volume of water in the lower bay, which supported a large contingent of anchovy larvae.

Survival and recruitment potential of anchovy cohorts were responsive to variability in both mortality rates and growth rates that they experienced. The ratio M/G, an index of stage-specific mortality, is an important indicator of comparative production and survival potential during early life (Houde, 1996,

1997a). The baywide M/G ratio for bay anchovy larvae declined from 1.59 in June to 0.67 in July. The low M/G ratio in July is a reflection of the coincident decline in larval mortality rate and increase in growth rate that occurred between June and July. The difference in M/G ratios between months implies a 70-fold higher survival potential through the larval stage for July-hatched cohorts.

M/G ratios <1.0, signifying high regional production potential, were observed in the mid bay in June and in the mid and upper bay in July. Larvae in those regions tended to have lowest mortality rates. An abundance of large larvae generally indicates higher survival rates of cohorts, but size-selective mortality or transport (or both) of larvae into a region (Fortier and Leggett, 1982, 1985; Norcross and Shaw, 1984; Boehlert and Mundy, 1988) could have contributed to the relative abundances of large larvae and low M/G ratios. In the Patuxent River subestuary of Chesapeake Bay, progressive increases in larval length upriver were reported by Loos and Perry (1991), who hypothesized (with supporting evidence) that transport of larvae was primarily responsible. Similarly, MacGregor and Houde (1996) reported a gradient in bay anchovy larval size on a cross-Bay transect that was repetitively sampled; smallest larvae were found offshore and largest larvae, inshore. In the present study, selective up-bay transport of larvae could have acted to reduce the M/G ratio in the upper bay between June and July, but we cannot confirm it.

In summary, mortality rates of bay anchovy early-life stages were both temporally and regionally variable at one-month temporal and at 60-km spatial scales in Chesapeake Bay. Growth rates showed strong temporal variation but no significant regional differences. Stage-specific survival, which depended upon both mortality and growth rates, was both size-specific and growth-rate dependent. We found no obvious indication of density-dependent mortality (i.e. no correlations between egg or larval abundances and mortality or growth rates), although recent individual-based modeling suggests that density-dependence in early-life could be an important regulator of bay anchovy recruitments in Chesapeake Bay (Wang et al., 1997). The lower Chesapeake Bay in July was the major source of potential recruits in 1993. Temperature, zooplankton prey, and gelatinous predators all are believed to have contributed to temporal and regional differences in growth and mortality of larvae. Further research is needed to define scales and patterns of processes that control variability in production and recruitment of bay anchovy. This will require coupled biophysical studies and development of models that, up to now, have essentially emphasized only biology.

Acknowledgments

Research was supported by National Science Foundation grants OCE-92-03307 and OCE95-21512 to E. D. Houde and by NSF Land Margin Ecosystem grant DEB94-12113 to W. R. Boynton et al. We thank the officers and crew of RV *Henlopen* for capable research-vessel support and numerous colleagues and students who assisted in the research. We especially thank S. Leach and L. Fernandez for assistance with illustrations and preparation of the manuscript.

Literature cited

Bailey, K. M., and E. D. Houde.
1989. Predation on early developmental stages of marine fishes and the recruitment problem. Adv. Mar. Biol. 25:1–83.

Baird, D., and R. E. Ulanowicz.
1989. The seasonal dynamics of the Chesapeake Bay ecosystem. Ecol. Monogr. 59(4):329–364.

Beyer, J. E.
1989. Recruitment stability and survival-simple size-specific theory with examples from the early life dynamics of marine fish. Dana 7:45–147.

Boehlert, G. W., and B. C. Mundy.
1988. Roles of behavior and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. Am. Fish. Soc. Symp. 3:51–67.

Bolz, G. R., and B. R. Burns.
1996. Age and growth of larval Atlantic herring, *Clupea harengus*: a comparative study. Fish. Bull. 94:387–397.

Castro, L. R., and R. K. Cowen.
1991. Environmental factors affecting the early life history of bay anchovy *Anchoa mitchilli* in Great South Bay, New York. Mar. Ecol. Prog. Ser. 76:235–247.

Cowan, J. H., Jr., and E. D. Houde.
1990. Growth and survival of bay anchovy *Anchoa mitchilli* larvae in mesocosm enclosures. Mar. Ecol. Prog. Ser. 68:47–57.
1992. Size-dependent predation on marine fish larvae by ctenophores, scyphomedusae and planktivorous fish. Fish. Oceanogr. 1:113–126.
1993. Relative predation potentials of scyphomedusae, ctenophores and planktivorous fish on ichthyoplankton in Chesapeake Bay. Mar. Ecol. Prog. Ser. 95:55–65.

Cushing, D. H.
1975. Marine ecology and fisheries. Cambridge Univ. Press, Cambridge, U.K, 278 p.

Dalton, P. D.
1987. Ecology of bay anchovy, *Anchoa mitchilli*, eggs and larvae in the mid-Chesapeake Bay. M.S. thesis, Univ. of Maryland, College Park, MD, 104 p.

Dorsey, S. E., E. D. Houde, and J. C. Gamble.
1996. Cohort abundances and daily variability in mortality of eggs and yolk-sac larvae of bay anchovy, *Anchoa mitchilli*, in Chesapeake Bay. Fish. Bull. 94:257-267.

Dovel, W. L.
1971. Fish eggs and larvae of the upper Chesapeake Bay. Natural Resources Inst., Univ. of Maryland Special Report 4, 71 p.

Feigenbaum, D., and M. Kelly.
1984. Changes in the lower Chesapeake Bay food chain in

presence of the sea nettle *Chrysaora quinquecirrha* (schyphomedusa). Mar. Ecol. Prog. Ser. 19:39–47.

Fives, J. M., S. M. Warlen, and D. E. Hoss.
1986. Aging and growth of larval bay anchovy *Anchoa mitchilli*, from the Newport River Estuary, North Carolina. Estuaries 9:362-367.

Fortier, L., and W. C. Leggett.
1982. Fickian transport and the dispersal of fish larvae in estuaries. Can. J. Fish. Aquat. Sci. 39:1150-1163.
1985. A drift study of larval fish survival. Mar. Ecol. Prog. Ser. 25:245–257.

Gallagher, R. P., M. F. Hirshfield, and E. S. Perry.
1983. Age, growth, and mortality estimates for larval bay anchovy *Anchoa mitchilli* in the Patuxent River. Benedict Estuarine Research Laboratory publication, Division of Environmental Research; Academy of Natural Sciences of Philadelphia, Philadelphia. PA, 34 p.

Hartman, K. J., and S. B. Brandt.
1995. Comparative energetics and the development of bioenergetics models for sympatric estuarine piscivores. Can. J. Fish. Aquat. Sci. 52:1647–1666.

Heath, M. R.
1992. Field investigations of the early life stages of marine fish. Adv. Mar. Biol. 28:3-174.

Hildebrand, S. F., and W. C. Schroeder.
1928. Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43:108–110.

Houde, E. D.
1978. Critical food concentrations for larvae of three species of subtropical marine fishes. Bull. Mar. Sci. 28:395–411.
1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2:17–29.
1989a. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. Bull. 87:471–495.
1989b. Subtleties and episodes in the early life of fishes. J. Fish Biol. 35 (suppl. A):29–38.
1996. Evaluating stage-specific survival during the early life of fish. *In* Y. Watanabe, Y. Yamashita and Y. Oozeki (eds.), Survival strategies in early life stages of marine resources, p. 51–66. Balkema, Rotterdam.
1997a. Patterns and consequences of selective processes in teleost early life histories. *In* R. C. Chambers and E. A. Trippel (eds.), Early life history and recruitment of fish populations, p. 173–196. Chapman and Hall, London.
1997b. Patterns and trends in larval-stage growth and mortality of teleost fish. J. Fish Biol. 51(suppl. A):52–83.

Houde, E. D., and C. E. Zastrow.
1991. Bay anchovy. *In* S. L. Funderburk, J. A. Mihursky, S. J. Jordan, and D. Riley (eds.), Habitat requirements for Chesapeake Bay living resources, 2nd ed., p. 8-1 to 8-14. Living Resources Subcommittee, Chesapeake Bay Program, Annapolis, MD.

Leak, J. C.
1986. The relationship of standard length and otolith diameter in larval bay anchovy, *Anchoa mitchilli*, a shrinkage estimator. J. Exp. Mar. Biol. Ecol. 95:167–172.

Leak, J. C., and E. D. Houde.
1987. Cohort growth and survival of bay anchovy *Anchoa mitchilli* larvae in Biscayne Bay, Florida. Mar. Ecol. Prog. Ser. 37:109–122.

Leggett, W. C.
1986. The dependence of fish larval survival on food and predator densities. *In* The role of freshwater outflow in coastal marine ecosystems, p. 118–137. NATO ASI series, vol. G7.

Leggett, W. C., and E. DeBlois.
1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? Netherlands J. Sea Res. 32:119–134.

Loos, J. J., and E. S. Perry.
1991. Larval migration and mortality rates of bay anchovy in the Patuxent River. U.S. Dep. Commer., NOAA Technical Report NMFS 95:65–76.

Luo, J., and J. A. Musick.
1991. Reproductive biology of the bay anchovy in Chesapeake Bay. Trans. Am. Fish. Soc. 120:701–710.

MacGregor, J. M.
1994. Temporal and spatial variability in cross-bay distribution and abundance of bay anchovy (*Anchoa mitchilli*) eggs and larvae. M.S. thesis, Univ. Maryland, College Park, MD, 138 p.

MacGregor, J. M., and E. D. Houde.
1996. Onshore-offshore pattern and variability in distribution and abundance of bay anchovy *Anchoa mitchilli* eggs and larvae in Chesapeake Bay. Mar. Ecol. Prog. Ser. 138:5–25.

Monteleone, D. M., and L. E. Duguay.
1988. Laboratory studies of predation by the ctenophore Mnemiopsis leidyi on the early stages in the life history of the bay anchovy, *Anchoa mitchilli*. J. Plankton Res. 10:359–372.

Newberger, T. A., and E. D. Houde.
1995. Population biology of bay anchovy, *Anchoa mitchilli*, in mid-Chesapeake Bay. Mar. Ecol. Prog. Ser. 116:25–37.

Norcross, B. L., and R. F. Shaw.
1984. Oceanic and estuarine transport of fish eggs and larvae: a review. Trans. Am. Fish. Soc. 113:153–165.

Olney, J. E.
1983. Eggs and early larvae of the bay anchovy, *Anchoa mitchilli*, and the weakfish, *Cynoscion regalis*, in lower Chesapeake Bay with notes on associated ichthyoplankton. Estuaries 6(1):20–35.

Pepin, P.
1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Can. J. Fish. Aquat. Sci. 48:503–518.

Purcell, J. E. and J. H. Cowan, Jr.
1995. Predation by the scyphomedusan *Chrysaora quinquecirrha* on *Mnemiopsis leidyi* ctenophores. Mar. Ecol. Prog. Ser. 129:63–70.

Purcell, J. E., D. A. Nemazie, S. E. Dorsey, E. D. Houde, and J. C. Gamble.
1994. Predation mortality of bay anchovy (*Anchoa mitchilli*) eggs and larvae due to scyphomedusae and ctenophores in Chesapeake Bay. Mar. Ecol. Prog. Ser. 114:47–58.

SAS Institute.
1990. SAS/STAT user's guide, version 6, fourth ed, vols. I and II. SAS Institute, Cary, NC, 245 p.

Secor, D. H., J. M. Dean, and E. H. Laban.
1991. Manual for otolith removal and preparation for microstructure examination. Univ. South Carolina, Columbia, SC, 85 p.

Theilacker, G. H.
1980. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. Fish. Bull. 78(3):685–692.

Wang, S.-B., J. H. Cowan Jr., K. A. Rose, and E. D. Houde.
1997. Individual-based modelling of recruitment variability and biomass production of bay anchovy in mid-Chesapeake Bay. J. Fish Biol. 51(suppl. A):101-120.

Wang, S,-B., and E. D. Houde.
1995. Distribution, relative abundance, biomass and production of bay anchovy *Anchoa mitchilli* in the Chesapeake Bay. Mar. Ecol. Prog. Ser. 121:27–38.

Zastrow, C. E., E. D. Houde, and L. G. Morin.
1991. Spawning, fecundity, hatch-date frequency and young-of-the-year growth of bay anchovy, *Anchoa mitchilli* in mid-Chesapeake Bay. Mar. Ecol. Prog. Ser. 73:161–171.

Estimation of size at sexual maturity: an evaluation of analytical and resampling procedures

Rubén Roa
Departamento de Oceanografía
Universidad de Concepción
Casilla 160-C, Concepción, Chile
E-mail address: rroa@udec.cl

Billy Ernst
School of Fisheries, WH-10
University of Washington, Seattle, Washington 98195

Fabián Tapia
Departamento de Oceanografía
Universidad de Concepción
Casilla 160-C, Concepción, Chile

Abstract.–Size at 50% maturity is commonly evaluated for wild populations, but the uncertainty involved in such computation has been frequently overlooked in the application to marine fisheries. Here we evaluate three procedures to obtain a confidence interval for size at 50% maturity, and in general for *P*% maturity: Fieller's analytical method, nonparametric bootstrap, and a Monte Carlo algorithm. The three methods are compared in estimating size at 50% maturity ($l_{50\%}$) by using simulated data from an age-structured population, with von Bertalanffy growth and constant natural mortality, for sample sizes of 500 to 10,000 individuals. Performance was assessed by using four criteria: 1) the proportion of times that the confidence interval did contain the true and known size at 50% maturity, 2) bias in estimating $l_{50\%}$, 3) length and 4) shape of the confidence interval around $l_{50\%}$. Judging from criteria 2–4, the three methods performed equally well, but in criterion 1, the Monte Carlo method outperformed the bootstrap and Fieller methods with a frequency remaining very close to the nominal 95% at all sample sizes. The Monte Carlo method was also robust to variations in natural mortality rate (M), although with lengthier and more asymmetric confidence intervals as M increased. This method was applied to two sets of real data. First, we used data from the squat lobster *Pleuroncodes monodon* with several levels of proportion mature, so that a confidence interval for the whole maturity curve could be outlined. Second, we compared two samples of the anchovy *Engraulis ringens* from different localities in central Chile to test the hypothesis that they differed in size at 50% maturity and concluded that they were not statistically different.

Manuscript accepted 28 August 1998.
Fish. Bull. 97:570–580 (1999).

Size at 50% maturity ($l_{50\%}$) is commonly evaluated for wild populations as a point of biological reference (see Table 1). To estimate $l_{50\%}$, a sample of organisms known to have just reached sexual maturity could be available and their arithmetic mean size can be used as an estimator. However, the sample needed to obtain such a design-based estimator (Smith, 1990) for wild populations might be too expensive and would involve time-consuming histological procedures. Fisheries biologists prefer to conceive size at first maturity as the average size at which 50% of the individuals are mature. With this conception, the estimator is not based on a sampling design but on a model of the relation between body size and the number of individuals that are mature from a total number at each of many size intervals. The variance of a design-based estimator is determined by sampling design (Thompson, 1992). The variance of a model-based estimator is not as easily obtained. A sample of published works in the fisheries literature provides a measure of the frequency with which statistical uncertainty of the model-based $l_{50\%}$ is ignored (Table 1). In this work, we show three alternative procedures: an analytical method derived from generalized linear models (McCullagh and Nelder, 1989), nonparametric bootstrap (Efron and Tibshirani, 1993), and a Monte Carlo algorithm developed in our study. We show by simulation the behavior of the three methods for sample sizes of 500 to 10,000 individuals, concluding that they are similar in terms of bias, length, and shape of confidence intervals but that the Monte Carlo method outperforms the other two methods in percentage of times that the confidence interval contains the true parameter, which remained close to the nominal 95% at all sample sizes.

The problem

In regression analysis, we are usually interested in assigning confidence bounds to the response variable at specified levels of the predictor variable. However, in maturity modeling the attention is turned to the converse problem of

Table 1

An example of published analyses on size at maturity in crustacean and fish populations. CW = carapace width; CL = carapace length; TL = total length; m = males; f = females; [g] = gonadal maturity; [m] = morphometric maturity.

Paper	Species	Fitting method	$l_{50\%}$ (mm)	CI 95%	CI estimation method
Somerton (1980)	*Paralithodes camtschatica* *Chionoecetes bairdi*	Weighted nonlinear least-squares	102.8 (CL, m) 101.9 (CL, f) 114.7 (CW, m)	Not reported Not reported Not reported	Random partition of data into subsets and computation of var ($l_{50\%}$) among the N independent estimates of $l_{50\%}$
Campbell and Robinson (1983)	*Homarus americanus*	Nonlinear least-squares	108.1 (CL, f) 92.5 (CL, f) 78.5 (CL, f)	— — —	— — —
Somerton and MacIntosh (1983)	*Paralithodes platypus*	Weighted nonlinear least-squares	80.6 (CL, f) 96.3 (CL, f) 93.7 (CL, f) 87.4 (CL, f)	79.4–82.6 95.7–96.9 92.9–94.5 86.4–88.4	Random partition of data into subsets and computation of var ($l_{50\%}$) among the N independent estimates of $l_{50\%}$
Campbell and Eagles (1983)	*Cancer irroratus*	Nonlinear least-squares	62.0 (CW, m) 49.0 (CL, f)	— —	— —
Somerton and Otto (1986)	*Lithodes aequispina*	Weighted nonlinear least-squares	97.7 (CL, f) 99.0 (CL, f) 110.7 (CL, f) 92.0 (CL, m) 107.0 (CL, m) 130.0 (CL, f)	Values not reported	Bootstrap samples were drawn from the original data set for obtaining independent estimates of $l_{50\%}$, and then computing var($l_{50\%}$) among them.
Gaertner and Laloé (1986)	*Geryon maritae*	Nonlinear least-squares	82.8 (CL, f)	—	Confidence regions for the parameters of a logistic function were computed.
Comeau and Conan (1992)	*Chionoecetes opilio*	Nonlinear least-squares	34.2 (CW, m)	—	—
Armstrong et al. (1982)	*Lophius americanus* (Pisces: Lophiiformes)	Linear regression of Prop. Mature (arcsine-square root transformed) on Total Length	368.9 (TL, m) 458.3 (TL, f)	— —	— —
Lovrich and Vinuesa (1993)	*Paralomis granulosa*	Probit	50.2 (CL, m)[g] 60.6 (CL, f)[g] 57.0 (CL, m)[m] 66.5 (CL, f)	— 58.3–62.9 53.9–60.1 63.4–69.5	— Not reported Not reported Not reported
Roa (1993a)	*Pleuroncodes monodon*	Maximum likelihood	27.2 (CL, f)	24.2–30.2	Ratio of parameter estimates confidence limits
González-Gurriarán and Freire (1994)	*Necora puber*	Maximum likelihood	54.8 CW, m)[g] 49.8 (CW, f)[g] 53.3 (CW, m)[m] 52.3 (CW, f)[m]	— — — —	— — — —

setting a confidence interval for the size at which a fixed proportion of individuals in a population are sexually mature. That is, we need a procedure for estimating uncertainty in the predictor variable because management decisions are framed in terms of body size, and hence the uncertainty in estimation

must be transferred to this variable. The first part of the problem is the selection of the maturity model. The available data consist of size (normally length) and maturity status, which will be assumed to take only two values: mature or immature. The predictor variable is continuous and the response variable is dichotomous. With such variables, model errors distribute binomially. Welch and Foucher (1988) recognized this aspect of modeling maturity and showed an efficient procedure based on the principle of maximum likelihood that takes advantage of the binomial nature of the errors.

For dichotomous data modeled as a function of a continuous variable, the following simple logistic function is a consequence of the assumption of a linear relationship between the logit link function and a single predictor variable (Shanubhogue and Gore, 1987; Hosmer and Lemeshow, 1989; McCullagh and Nelder, 1989):

$$P(l) = \frac{\alpha}{1+e^{\beta_0+\beta_1 l}}, \quad (1)$$

where $P(l)$ = proportion mature at size l; and
α, β_0, and β_1 = asymptote, intercept, and slope parameters, respectively (see also Eq. 3).

The estimates of these parameters, given a data set, are chosen from the point at which the product of binomial mass functions of all data points (the likelihood of the data under the model) is a maximum, or equivalently when the negative of the log likelihood

$$-l(\alpha,\beta_0,\beta_1) = -\sum_l \left[(h_l)\ln(P(l)) + (n_l - h_l)\ln(1-P(l))\right] \quad (2)$$

is a minimum,

where h = the number of mature individuals; and
n = sample size at l;
$P(l)$ = Eq. 1; and

where a constant term that does not affect the estimation is omitted.

Given the nonlinear nature of normal equations, the minimum is found by an iteration algorithm. The parameters estimated by minimizing Equation 2 are maximum likelihood estimates (MLE). In practical situations, the logistic model may be modified from its original form to allow more biological reality (Welch and Foucher, 1988).

The result from fitting the model (Eq. 1) to the data by using the objective in Equation 2, is a vector of parameter estimates and a covariance matrix, which represents the uncertainty associated to them. With these results, we may undertake the converse problem of estimating size at fixed $P\%$ maturity, which takes the form

$$l_{P\%} = \frac{1}{\beta_1}\ln\left[\frac{1}{P}-1\right] - \frac{\beta_0}{\beta_1}. \quad (3)$$

In Equation 3 it is assumed that the asymptote parameter (α) from Equation 1 is fixed at 1. This assumption is justified on the basis of several published works on size at maturity, showing that all individuals were mature above a given size during the reproductive season (Table 1). Furthermore, if $\hat{\beta}_0$ and $\hat{\beta}_1$ are MLE of β_0 and β_1 and they are used to compute $l_{P\%}$ from Equation 3, then $\hat{l}_{\%}$ is also MLE. We show below three procedures to perform this task and then test them by generating data from Monte Carlo simulation of the age-size structure and maturity progression of individuals of a hypothetical population.

Analytical estimation

The logistic model in Equation 1 belongs to a class of generalized linear models studied by McCullagh and Nelder (1989). These authors consider the problem of building approximate confidence intervals for the level of the predictor variable that gives rise to a fixed proportion in the response variable. They suggest the use of Fieller's (1944) theorem, according to which the linear combination

$$\beta_0 + \beta_1 l_{P\%} - g(P_0) = 0, \quad (4)$$

where $l_{P\%}$ = the value of the predictor variable for a fixed proportion; and $g(P_0)=ln(P_0/(1-P_0))$ (the logit link function) is approximately normal with mean zero and analytical variance given by

$$v^2(l_{P\%}) = \mathrm{var}(\hat{\beta}_0) + 2l_{P\%}\,\mathrm{cov}(\hat{\beta}_0,\hat{\beta}_1) + l_{P\%}^2\,\mathrm{var}(\hat{\beta}_1). \quad (5)$$

The $100(1-\alpha)\%$ confidence interval is the set of values defined by

$$\frac{1}{\hat{\beta}_1}\left(-\hat{\beta}_0 + g(P_0) \pm z_{\alpha/2}\, v(l_{P\%})\right), \quad (6)$$

where $z_{\alpha/2}$ = a quantile of the normal distribution.

Other link functions like probit, common in the field of toxicology (Finney, 1977), are not investigated in this paper.

Bootstrap estimation

Bootstrap is not a uniquely defined concept (Efron and Tibshirani, 1993). This means that bootstrap

samples may be obtained by conceptually different resampling procedures. In the context of logistic regression, it is possible to resample the observational pair (l_i, h_i), or the semiobservational pair $(l_i, P(l)+\varepsilon_i)$, with ε_i as a realization from the residual distribution of the logistic model. To be valid, this second resampling unit needs the assumption of independence between ε_i and l_i. As stated by Efron and Tibshirani (1993), this is a strong assumption that can fail even when the model $P(l)$ is correct. These authors remark that bootstrapping the observational pair is less sensitive to assumptions than bootstrapping residuals. Therefore, in our work an observation to be resampled with replacement is defined as the pair (length, maturity status). For each and all bootstrap samples, a resampled frequency distribution for l_{Pc_i} is obtained by fitting the maturity model in Equation 1 with the objective function in Equation 2 and by computing l_{Pc_i} with Equation 3. The confidence interval is obtained by application of the bias-corrected and accelerated (BCa) method, recommended by Efron and Tibshirani (1993).

Monte Carlo estimation

In Monte Carlo resampling, a model is assumed for the distribution of the estimator and then data are generated computationally to assess the amount of variation (Manly, 1997). In our case, we consider a Monte Carlo resampling of maturity parameters from the modeled joint probability distribution of the estimates $\hat{\beta}_0$ and $\hat{\beta}_1$ for computing $\hat{l}_{Pc_i}$ from Equation 3. In contrast to the bootstrap approach, the implementation of this approach needs only one fitting of the logistic maturity model and then uses the asymptotic distribution of estimated parameters of the model to generate the probability distribution of the derived statistic l_{Pc_i}. These parameter estimates, $\hat{\beta}_0$ and $\hat{\beta}_1$, distribute asymptotically bivariate normal, with mean vector equal to the population parameters and variance given by their covariance matrix (for nonlinear least-squares: Johansen, 1984; for maximum-likelihood estimates: Chambers, 1977). The bivariate normal distribution of $\hat{\beta}_0$ and $\hat{\beta}_1$ has a strong covariance component, which is the same as to say that these estimates are highly correlated. This also means that much of the variance in one estimate is given by the variance in the other one. Ignoring such correlation would lead to an overestimation of the variance of l_{Pc_i}. In a Monte Carlo setting, the correlation between parameter estimates may be considered in the computation by making the resampling of one estimate conditional on the resampling of the other one. In this work we develop such a technique using the theory of least-squares estimates of two linearly related normal variates (Draper and Smith, 1981). This approach is justified by the asymptotic nature of standard errors. If $\hat{\beta}_0$ and $\hat{\beta}_1$ and are two normal random variables that are linearly related, then we may write the linear equation

$$\hat{\beta}_1 = \hat{b}_0 + \hat{b}_1\hat{\beta}_0. \tag{7}$$

This equation may be reversed by writing $\hat{\beta}_0$ as a linear function of $\hat{\beta}_1$ because both are random variables. It can be shown that (Draper and Smith, 1981)

$$\hat{b}_1 = \hat{r}_{\hat{\beta}_0\hat{\beta}_1}\left[\frac{\hat{S}_{\hat{\beta}_1}}{\hat{S}_{\hat{\beta}_0}}\right], \tag{8}$$

where r is the estimated linear correlation coefficient between $\hat{\beta}_0$ and $\hat{\beta}_1$, and $S_{\hat{\beta}_0}$ and $S_{\hat{\beta}_1}$ are the respective standard errors. Furthermore, from Equation 7

$$\hat{b}_0 = \hat{\beta}_1 - \hat{b}_1\hat{\beta}_0. \tag{9}$$

Therefore, the high correlation coefficient between both maturity parameters can be accounted for by free sampling from the marginal distribution of one parameter estimate (for example, $\hat{\beta}_0$) in each Monte Carlo trial and by computing the other by using

$$\begin{aligned}\beta_{1,j} &= \hat{\beta}_1 - \hat{r}_{\hat{\beta}_0,\hat{\beta}_1}\left[\frac{\hat{S}_{\hat{\beta}_1}}{\hat{S}_{\hat{\beta}_0}}\right]\hat{\beta}_0 + \hat{r}_{\hat{\beta}_0,\hat{\beta}_1}\left[\frac{\hat{S}_{\hat{\beta}_1}}{\hat{S}_{\hat{\beta}_0}}\right]\beta_{0,j} \\ &= \hat{\beta}_1 + \hat{r}_{\hat{\beta}_0\hat{\beta}_1}\left[\frac{\hat{S}_{\hat{\beta}_1}}{\hat{S}_{\hat{\beta}_0}}\right]\left[\beta_{0,j} - \hat{\beta}_0\right]\end{aligned}, \tag{10}$$

which is obtained by replacing Equations 8 and 9 in Equation 7. For each trial (indexed by j), a β_0 value is selected from the normal probability distribution defined by its estimate and standard error, and then the mean β_1 value is computed by using Equation 10.

The variance of the estimate is the $\hat{\beta}_0$ variance due to the linear relationship with $\hat{\beta}_0$ plus a residual variance not explained by the relationship. The variance due to the relationship is directly transferred from $\hat{\beta}_0$ to $\hat{\beta}_1$ through the Monte Carlo resampling of $\hat{\beta}_0$ and its mapping onto $\hat{\beta}_1$ by using Equation 10. The residual variance must be added in each trial with

$$\hat{S}^2_{\hat{\beta}_1,residual} = \hat{S}^2_{\hat{\beta}_1}\left(1 - \hat{r}^2_{\hat{\beta}_0,\hat{\beta}_1}\right), \tag{11}$$

where $\hat{r}^2_{\hat{\beta}_0,\hat{\beta}_1}$ = the proportion of variance due to the linear relationship.

Note in Equation 10 that when r=0, the mean of the $\hat{\beta}_{1,j}$ for all j would just be the $\hat{\beta}_1$ estimate, which means that β_0 and β_1 values are independently selected in each trial; note also in Equation 11 that the resampling variance of the estimate would be its total variance. On the other hand, when $r=|1|$, Equation 11 shows that the resampling variance of β_1 would be totally due to the mapping of $\beta_{0,j}$ onto $\beta_{1,j}$, which is expected when the linear relationship between two variables is deterministic. In this case, the algorithm presented here would only perform one Monte Carlo simulation, that on β_0. Therefore, the algorithm is flexible enough to cover the whole range of correlation between both parameter estimates.

A confidence interval for $l_{P\%}$ may be obtained by the percentile method (Casella and Berger, 1990; Efron and Tibshirani, 1993), for which two computational alternatives are available. If the resampling through the bivariate normal distribution is unbounded, then the 100(1–α)% confidence interval is obtained by ordering the $l_{P\%,j}$ from smallest to largest, and taking as bounds the values at positions $N_{MC}(\alpha/2)$ and $N_{MC}(1-(\alpha/2)$, where N_{MC} is number of Monte Carlo trials. If the resampling through the bivariate normal distribution is bounded, with bounds $\alpha/2$ and $1-\alpha/2$, then the 100(1–α)% confidence interval limits are obtained as the first and last quantiles when ordering the $l_{P\%,j}$ from smallest to largest.

Monte Carlo simulation

To test the performance of the three procedures in estimating $l_{P\%}$ for different sample sizes, we carried out a simulation analysis of a model population with known size-at-age structure, maturity-at-size, and mortality parameters (Table 2). We explored only the behavior of the methods for median (50%) size at maturity ($l_{50\%}$). Performance was evaluated by using four criteria. First, as the proportion of times that confidence intervals did contain the true (and known) parameter ($l_{50\%}$), which we call success:

$$success = 1 - failure = 1 - \frac{number\{(true - lower)(upper - true) < 0\}}{number\ of\ iterations} \quad (12)$$

Our second criterion was bias, evaluated as the average, over trials, of the sufficient statistic:

Table 2

Parameter estimates used in the model to generate simulated data. Growth and maturity functions given by Roa (1993a) for female squat lobsters (*Pleuroncodes monodon*). Natural mortality rate (M) given by Roa (1993b) for the same species.

Parameter	Value
Size-at-age	
σ^2	4
Growth	
L	44.55
k (/yr)	0.179
t_0 (/yr)	–0.51
Maturity	
α	1
β_0	13.648
β_1	–0.502
$l_{50\%}$ (mm)	27.2
Natural mortality	
M (/yr)	0.6

$$bias = \frac{resampled\ median}{true}, \quad (13)$$

which is 1 for an unbiased estimator. The third criterion was the length of confidence intervals:

$$length = upper - lower, \quad (14)$$

and the fourth and final criterion was the shape of the interval (Efron and Tibshirani, 1993):

$$shape = \frac{upper - median}{median - lower}, \quad (15)$$

which measures asymmetry around the median. In all four measures of performance, "upper" and "lower" refer to the bounds of the confidence interval, "median" is the median $l_{P\%}$, and "true" refers to the true value. The deterministic and stochastic features of our simulation were chosen for a population with features like those previously reported for the squat lobster (*Pleuroncodes monodon*) from the continental shelf off central Chile (Roa, 1993a, 1993b).

To accomplish this task, we implemented the following three-step algorithm, which we called MATSIMVL: step 1, generation of N_{iter}=5000 random samples of maturity-at-size data of sample size N_{sample}= 500, 1000, 3000, 5000, and 10,000 individuals (Eqs. 16–19); step 2, estimation of the parameter vector and covariance matrix for each one of these samples (Eqs. 1 and 2); and step 3, running each of the three methods to obtain the 2.5%, 50%, and 97.5%

percentiles of $l_{50\%}$ (Eqs. 3–11) In bootstrap, for each sample size and each of the 5000 trials, we obtained N_{boot}=5000 bootstrap samples. With the Monte Carlo method, we resampled parameter estimate values from unbounded normal distributions with N_{MC}= 5000. For completeness, $N_{Fieller}$=1.

In step 1, the deterministic size structure of the population was conceived as a mixture of normal probability distributions, each normal distribution corresponding to an age class. The proportion of individuals at each size interval was characterized by the following expression

$$p_{n_l} = \frac{\sum_{t=0}^{9} \frac{p_{n_t}}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{1}{2}\left(\frac{1-\mu_t}{\sigma}\right)^2\right]}{\sum_{l=0}^{40}\sum_{t=0}^{9} \frac{p_{n_t}}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{1}{2}\left(\frac{l-\mu_t}{\sigma}\right)^2\right]}, \quad (16)$$

where the sum is over 10 age classes (0 to 9) and 41 size classes (0 to 40), and where μ_t is determined by a growth equation

$$\mu_t = \mu_\infty\left(1-e^{-k(t-t_0)}\right) \quad (17)$$

with known parameters (Table 2). Variance of size-at-age (σ^2) is known and constant through age (Table 2), and the proportion of individuals at age (P_{nt}) is given by a simple exponential mortality model

$$P_{n_t} = \frac{e^{-Mt}}{\sum_{t=0}^{9} e^{-Mt}}, \quad (18)$$

where the mortality rate (M) is known and constant through age (Table 2).

Random variability came from two sources. First, samples of the specified sizes were drawn, for each trial, from a uniform probability distribution and compared with the cumulative distribution of Equation 16, accumulating the scores in the respective size intervals. This computation yielded a sample of relative size frequencies p_{nl}. Next, we introduced the second source of uncertainty by assessing the maturity status (mature or immature) of individuals belonging to each size class. This random assignment of maturity status came from resampling the binomial probability distribution

$$P(n = n_{rand}) = \binom{n_{l,rand}}{n_{rand}} P(l)^{n_{rand}}\left(1-P(l)^{(n_{l,rand}-n_{rand})}\right), \quad (19)$$

where $P(l)$ was computed from the logistic model (Eq. 1) with known maturity parameters (Table 2) and n_{rand} is the random number of mature individuals out of $n_{l,rand}=N_{sample}\times p_{nl}$ individuals in the size interval l. In this way, step 1 was completed by randomly assigning two properties to each data individual: a size (continuous variable) and a maturity status (dichotomous variable). With these data, step 2 was completed by using a nonlinear parameterization of the logistic model (Eqs. 1 and 2) for obtaining estimates of β_0 and β_1, and their covariance matrix, by means of the SIMPLEX algorithm (Press et al., 1992). Having this information in hand, step 3 was completed by obtaining 2.5%, 50%, and 97.5% percentiles by each of the three methods. We programmed the MATSIMVL algorithm using Microsoft FORTRAN for PowerStation 4.0 (Microsoft Corp., 1995).

In the case of the Monte Carlo algorithm, we also investigated the effect of the natural mortality parameter, by varying its level in simulation at M=0.2, M=0.4, M=0.6, and M=0.8, for sample sizes of N_{sample}=1000 and 5000 individuals. N_{iter} and N_{MC} were both kept at 5000.

Finally, we introduce real data to show two applications of the Monte Carlo method developed here. First, we estimate $l_{P\%}$ (N_{MC}=5000) for a single population of the galatheid decapod *Pleuroncodes monodon*. In this application, we estimate size confidence intervals for percentages of maturity from 10% to 90% at steps of 10%. In this way a confidence interval for the whole maturity curve is outlined. Second, we compare samples of female anchovy *Engraulis ringens* from two localities 3° of latitude apart (N_{MC}=5000) to test the null hypothesis of equal $l_{50\%}$ between them.

Results

The simulation analysis with MATSIMVL yielded size-at-age and maturity-at-size data with the appropriate behavior as N_{sample} increased: size-frequency distributions became smoother and maturity data more closely followed a logistic curve, as shown by one example output of MATSIMVL data-simulating routines (Fig. 1).

A summary of the simulation results is presented in Fig. 2. It shows that, under the simulation conditions, the Monte Carlo method outperformed the bootstrap and the Fieller methods in proportion of success at all sample sizes and that it remained very close to the nominal 95%; the bootstrap method succeeded 94% or less at all sample sizes, whereas the Fieller method was unstable between sample sizes of 500 to 5000, with a minimum of 93% success at 3000 (Fig. 2A). All three methods showed negligible

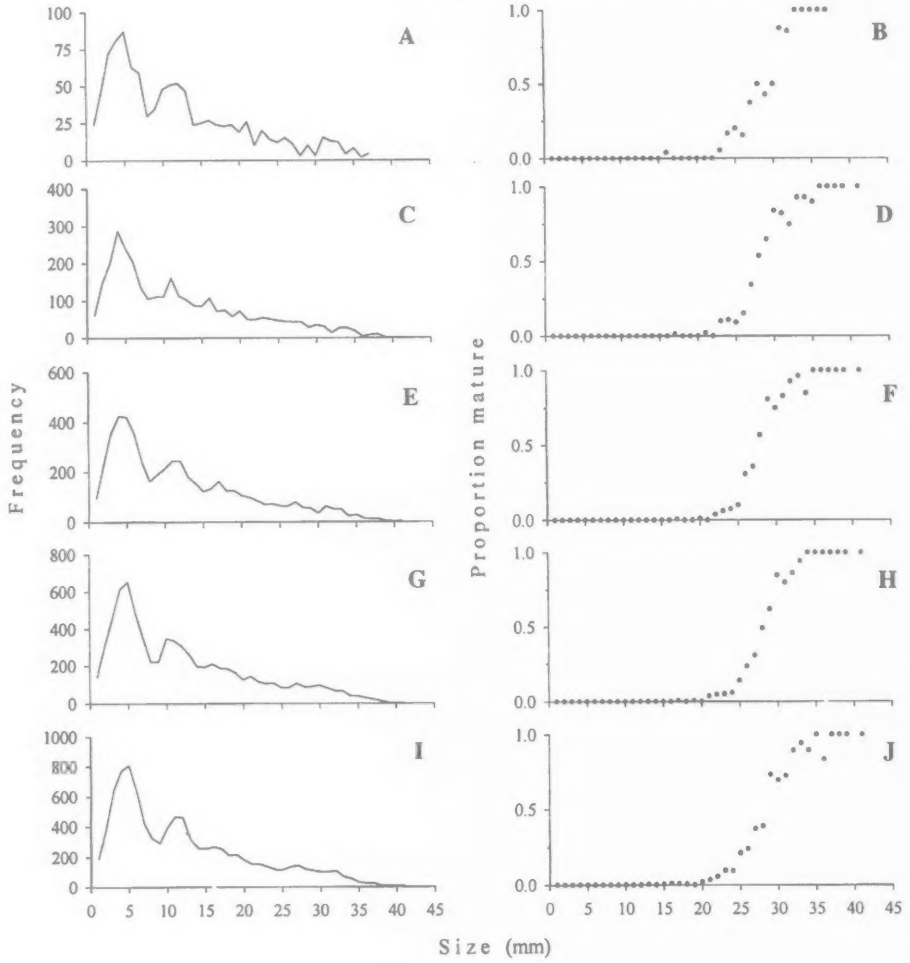


Figure 1

Example output of simulated data on size frequency and maturity-at-size generated by one trial of the MATSIMVL algorithm, for sample sizes of 500 (**A** and **B**), 1000 (**C** and **D**), 3000 (**E** and **F**), 5000 (**G** and **H**), and 10,000 (**I** and **J**) individuals.

bias at low sample sizes and converged neatly to null bias at large sample sizes (Fig. 2C). Likewise, the three methods behaved exactly the same in length of confidence interval, decaying exponentially as sample size increased (Fig. 2C). Finally, both resampling methods yielded asymmetrical (right-tailed) confidence intervals, converging to the same shape value (ca. 1.1) as sample size increased (by definition, Fieller's method yields a symmetrical confidence interval with shape=1).

Percentage success and bias of the Monte Carlo method under our model for data generation were fairly insensitive to changes in natural mortality M (Fig. 3) for sample sizes of 1000 and 5000 individuals. Percentage success remained close to the nominal 95% and bias was negligible. The length of the confidence interval and asymmetry, however, increased with increasing mortality, showing that estimation variance was directly proportional to natural mortality rate.

Results of the Monte Carlo algorithm with real data on female squat lobster are shown in Figure 4. The Monte Carlo confidence interval for $l_{50\%}$ was fairly narrow (25.86 to 28.51 mm carapace length),

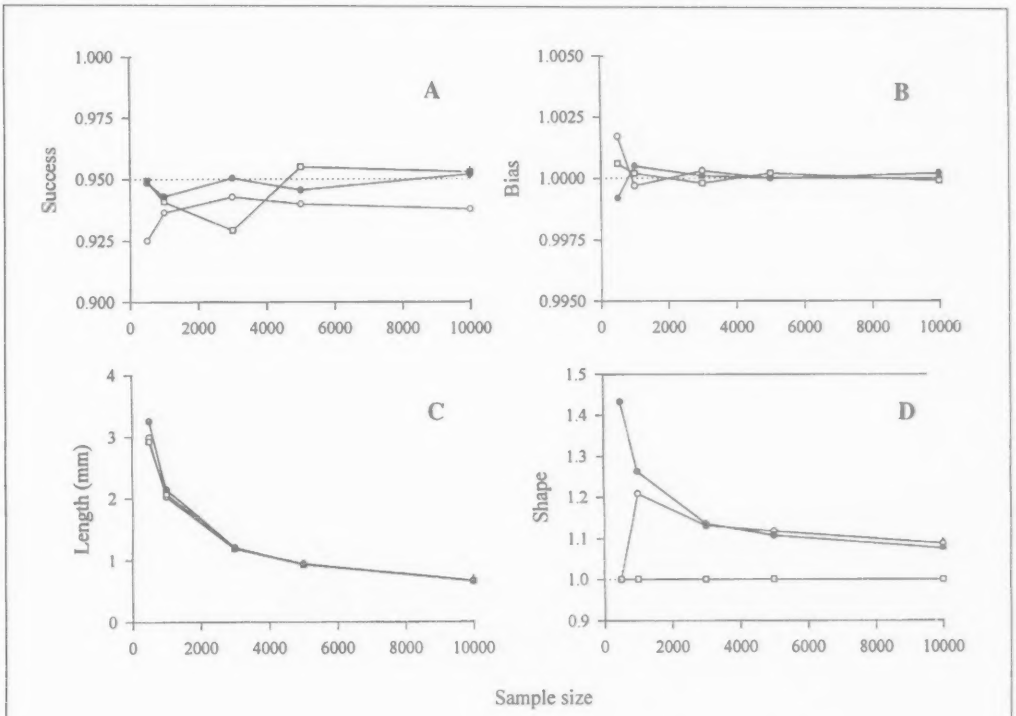


Figure 2

Summary of results from the application of the three methods to simulated data. Open squares = Fieller's analytical method; open circles: bootstrap; closed circles = Monte Carlo.

reflecting the effect of large sample size (N_{sample}= 4458). The Monte Carlo median $l_{50\%}$ (27.19 mm carapace length) coincided with the MLE of $l_{50\%}$=–MLE (β_0)(MLE(β_1). The amplitude of the confidence interval for $l_{P\%}$ showed an increasing trend towards extreme values of P (Fig. 4), a reflection of the algebraic structure of Equation 3. Results of the second application with two samples of female anchovies are shown on Figure 5. Although different in their lengths, probably due to different sample sizes, confidence intervals from the two samples overlapped and have the same upper limit. This result provides support to the hypothesis of equal maturity schedules between female anchovies from the two localities.

Discussion

The logistic model is universally used as a mathematical description of the relation between body size and sexual maturity. To model residuals, however, two different approaches emerge: to consider them normally or binomially distributed, and closely related to this, to use the data as proportions or as counts. In the first (as far as we know) formal treatment of the problem, Leslie et al. (1945) used the data as proportions, transformed to probit scores, and assumed the normal distribution. Current researchers have not employed probit transformations (but see Lovrich and Vinuesa, 1993) but have continued using data as proportions and the normal distribution for residuals (Table 1). In this work however, and following the arguments by Welch and Foucher (1988), we emphasize the need to estimate the maturity model using the data as counts and therefore to consider residuals as binomially distributed. Under this approach, the standard procedure for fitting the maturity model is logistic regression (Hosmer and Lemeshow, 1989).

When the model has been fitted, the problem of setting a confidence interval for the level of the predictor variable (size) that gives rise to a fixed proportion of maturity is not trivial. We have explored here three approaches: one analytical method based

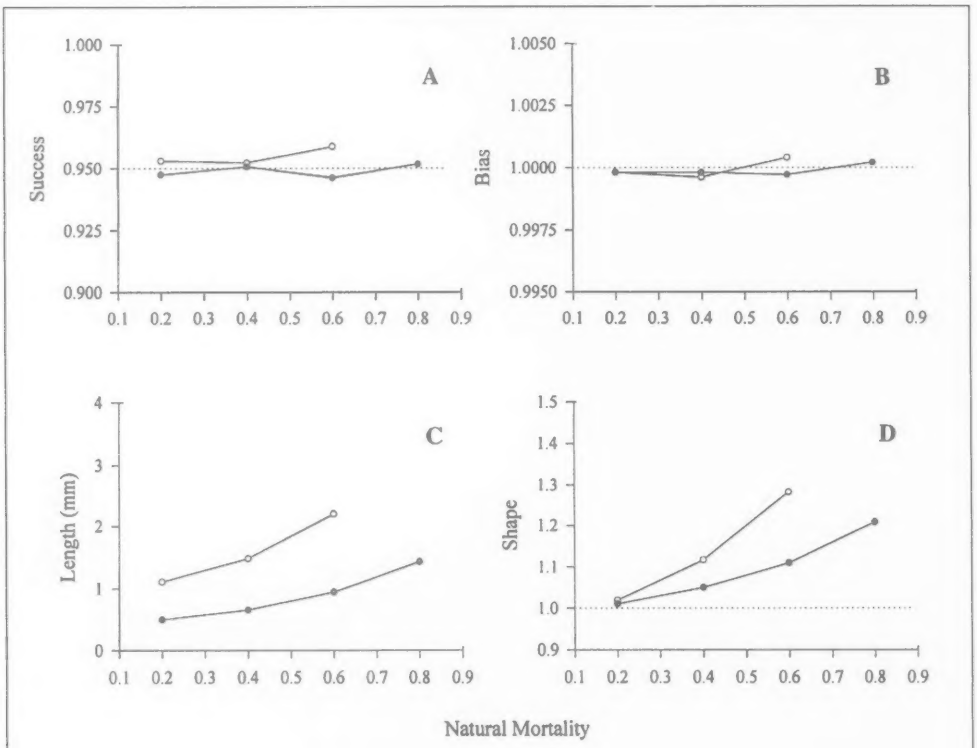


Figure 3

Effect on natural mortality rate on the performance of the Monte Carlo method. Open circles =1000 individuals; closed circles = 5000 individuals. N_{sample}= 5000, N_{MC}= 5000.

on Fieller's (1944) theorem and the logit link function, and two computationally-intensive methods based on nonparametric bootstrap of the observational pair (l_i, h_i) and Monte Carlo resampling of parameter estimates from the logistic model. Although this is not an exhaustive set of methods (for example, we did not explore likelihood profiles), they represent a set of conceptually different alternatives to be tested against the model we used to generate simulated data. In particular, both resampling methods are especially useful to obtain the distribution of a function of estimated parameters, such as in Equation 3, mainly because of their mathematical simplicity, which comes at the expense of extensive computation. Our results indicate that the three methods to estimate size at P% maturity perform almost equally well in terms of bias, length, and shape of the confidence interval, but that Monte Carlo performed better in containing the true parameter within its confidence bounds with the nominal 95% rate. This greater accuracy is accompanied by N_{boot}–1 times less computation than bootstrap.

Bootstrap single assumption was that all observations from any given sample have the same probability to appear in a new sample. In contrast, the Monte Carlo method assumed a bivariate normal distribution of parameter estimates of the maturity model. Having simpler assumptions, it is unclear why the bootstrap method failed more than the nominal 5% of the times at low sample sizes. One reasonable explanation is that for every sample, there would be N_{boot} bootstrap samples, and therefore N_{boot} numerical solutions to the normal equations under the binomial likelihood model. We used here 5000 bootstrap samples and the SIMPLEX algorithm (Press et al., 1992). Small errors in the numerical algorithm coupled with a minimum bias, may add to the nominal 5%, accounting for the 1% to 2% increase in failure rate. In contrast, the Monte Carlo algorithm requires a single numerical solution so that it does not accumulate numerical errors. On the other hand, Fieller's analytical method requires a more complicated set of assumptions than the Monte Carlo approach. Fieller's method requires normality of a lin-

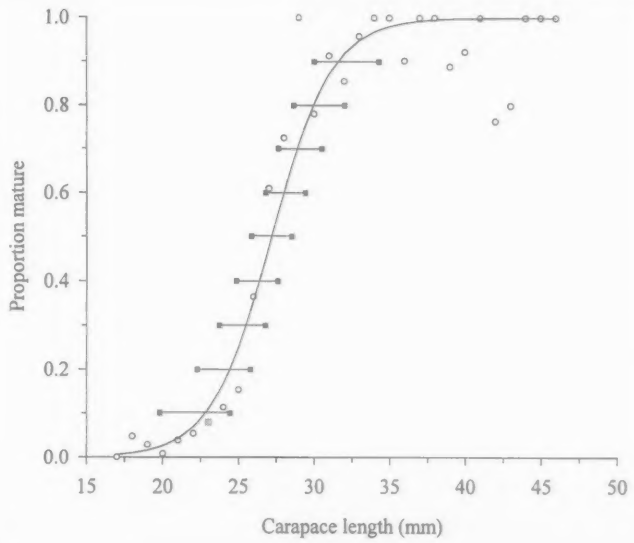


Figure 4

Monte Carlo confidence intervals for $P\%$ maturity for female squat lobsters, *Pleuroncodes monodon* (N_{sample}=4458, N_{MC}=5000). Open circles = raw data; continuous line = fitted model; closed squares = Monte Carlo confidence bounds for length at $P\%$ maturity (P=0.0–1.0 in steps of 0.1).

ear combination of parameter estimates and therefore assumes a symmetric interval estimate. Both bootstrap and Monte Carlo results indicate that the interval estimate can be quite asymmetric. This may account for the better performance of Monte Carlo, as compared with Fieller's, in proportion of success. These remarks, along with the facts that Monte Carlo's percentage success and bias are not affected by a natural mortality rate varying between 0.2 and 0.8, and that it is very fast on every computer platform, allows us to recommend the use of the Monte Carlo method to estimate size at $P\%$ maturity.

Acknowledgments

We would like to thank Bryan F. J. Manly for reviewing an earlier draft of this work and three anonymous reviewers who made several comments and criticisms which greatly improved the manuscript. This work was funded by FONDECYT grant 1950090 to R.R.

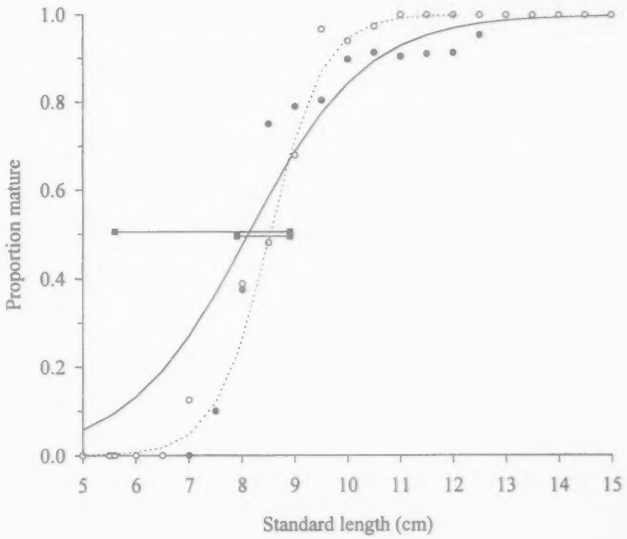


Figure 5

Monte Carlo confidence intervals for length at 50% maturity of female anchovies (*Engraulis ringens*) sampled from two localities off central Chile. Open circles and dotted line = Talcahuano (36°45'S) (N_{sample}=783, N_{MC}=5000); Closed circles and solid line = San Antonio (33°35'S) (N_{sample}=585, N_{MC}=5000); Closed squares = 95% confidence bounds for $l_{50\%}$.

Literature cited

Armstrong, M. P., J. A. Musick, and J. A. Convocoresses.
1992. Age, growth, and reproduction of the goosefish *Lophius americanus* (Pisces: Lophiiformes). Fish. Bull. 90:217–230.

Campbell, A., and M. D. Eagles.
1983. Size at maturity and fecundity of rock crabs, *Cancer irroratus*, from the Bay of Fundy and southwestern Nova Scotia. Fish. Bull. 81(2):357–362.

Campbell, A., and D. G. Robinson.
1983. Reproductive potential of three American lobster (*Homarus americanus*) stocks in the Canadian maritimes. Can. J. Fish. Aquat. Sci. 40:1958–1967.

Casella, G., and R. L. Berger.
1990. Statistical inference. Brooks and Cole Publ. Co., Duxbury, California. 650 p.

Chambers, J. M.
1977. Computational methods for data analysis. John Wiley and Sons, New York, NY, 268 p.

Comeau, M., and G. Y. Conan.
1992. Morphometry and gonad maturity of male snow crab, *Chionoecetes opilio*. Can. J. Fish. Aquat. Sci., 49:2460–2468.

Draper, N. R., and H. Smith.
1981. Applied regression analysis. John Wiley and Sons, New York, NY, 736 p.

Efron, B., and R. J. Tibshirani.
1993. An introduction to the bootstrap. Chapman & Hall, New York, NY, 436 p.

Fieller, E. C.
1944. A fundamental formula in the statistics of biological assay, and some applications. Quart. J. Pharm. 17:117–123.

Finney, D. J.
1977. Probit analysis, 3rd ed. Cambridge Univ. Press, New York, NY, 333 p.

Gaertner, D., and F. Laloé.
1986. Étude biométrique de la taille à première maturité sexuelle de *Geryon maritae* Manning et Holthuis, 1981 du Sénégal. Oceanol. Acta 9:479–487.

González-Gurriarán, E., and J. Freire.
1994. Sexual maturity in the velvet swimming crab *Necora puber* (Brachyura, Portunidae): morphometric and reproductive analyses. ICES J. Mar. Sci., 51:133–145.

Hosmer, D. W., and S. Lemeshow.
1989. Applied logistic regression. John Wiley and Sons, New York, NY, 328 p.

Johansen, S.
1984. Functional relations, random coefficients, and nonlinear regression with application to kinetic data. Springer-Verlag, New York, NY, 126 p.

Leslie, P. H., J. S. Perry, and J. S. Watson.
1945. The determination of the median body-weight at which female rats reach maturity. Proc. Zool. Soc. Lond. 115:473–488.

Lovrich, G. A., and J. H. Vinuesa.
1993. Reproductive biology of the false southern king crab (*Paralomis granulosa*, Lithodidae) in the Beagle Channel, Argentina. Fish. Bull. 91:664–675.

Manly, B. F. J.
1997. Randomization, bootstrap and Monte Carlo methods in biology, 2nd ed. Chapman & Hall, London, 399 p.

Microsoft Corp.
1995. FORTRAN PowerStation programmer's guide. Printed in the USA, 752 p.

McCullagh, P., and J. A. Nelder.
1989. Generalized linear models. Chapman & Hall, London. 511 p.

Press, W. H., S. A. Teukolsky, W. T. Vettering, and B. P. Flannery.
1992. Numerical recipes in FORTRAN, 2nd ed. Cambridge Univ. Press, Cambridge, 963 p.

Roa, R.
1993a. Annual growth and maturity function of the squat lobster *Pleuroncodes monodon* in central Chile. Mar. Ecol. Prog. Ser. 97:157–166.
1993b. Análisis metodológico pesquería de langostino colorado. Tech. Rep., Instituto de Fomento Pesquero (IFOP), Chile. 86 p. [Available from Subsecretaría de Pesca, Bellavista 168, piso 19, Valparaíso, Chile.]

Shanubhogue, A., and P. A. Gore.
1987. Using logistic regression in ecology. Curr. Sci. 56: 933–936.

Smith, S. J.
1990. Use of statistical models for the estimation of abundance from groundfish trawl survey data. Can. J. Fish. Aquat. Sci. 47:894–903.

Somerton, D. A.
1980. A computer technique for estimating the size of sexual maturity in crabs. Can. J. Fish. Aquat. Sci., 37:1488–1494.

Somerton, D. A., and R. A. MacIntosh.
1983. The size at sexual maturity of blue king crab, *Paralithodes platypus*, in Alaska. Fish. Bull. 81(3):621–628.

Somerton, D. A., and R. S. Otto.
1986. Distribution and reproductive biology of the golden king crab, *Lithodes aequispina*, in the eastern Bering Sea. Fish. Bull. 84(3):571–584.

Thompson, S. K.
1992. Sampling. John Wiley & Sons, New York, NY, 343 p.

Welch, D. W., and R. P. Foucher.
1988. A maximum likelihood methodology for estimating length-at-maturity with application to Pacific cod (*Gadus macrocephalus*) population dynamics. Can. J. Fish. Aquat. Sci. 45:333–343.

Spatial and temporal variability in growth, mortality, and recruitment potential of postsettlement red drum, *Sciaenops ocellatus*, in a subtropical estuary*

Jay R. Rooker

Scott A. Holt

G. Joan Holt

Lee A. Fuiman

Marine Science Institute
The University of Texas at Austin
750 Channelview Drive
Port Aransas, Texas 78373
Present address (for J. R. Rooker): Department of Marine Biology
Texas A&M University
5007 Avenue U
Galveston, Texas 77551
E-mail address (for J. R. Rooker): rookerj@tamug.tamu.edu

Abstract.—Patterns of growth and mortality were examined for postsettlement red drum, *Sciaenops ocellatus*, inhabiting seagrass meadows in the Aransas Estuary, Texas. Age and growth rates of larvae and early juveniles were estimated in 1994 and 1995 by using daily increments in otoliths. Otolith-derived estimates of age indicated that individuals spend approximately 20 d in the pelagic environment before entering demersal habitats (i.e. before settlement). Instantaneous growth coefficients (g) of red drum ranged from 0.049 (4.8%/d) in 1994 to 0.051 (5.0%/d) in 1995. Site-specific differences in growth were also examined and a significant site effect was detected in 1994; however, no site effect was observed in 1995. Interannual and cohort-specific (10-d cohorts) mortality rates were estimated from declines in $\log_e$ abundance (abundance-at-age plots), and results indicated that mortality during the early postsettlement period was substantial. Instantaneous mortality coefficients (Z) were similar between years (0.134 [12.5%/d] in 1994; 0.139 [13.0%/d] in 1995), and no significant interannual effect was observed. Conversely, cohort-specific mortality rates ranged widely (0.106–0.265 [10.1–23.3%/d]) and losses were lowest for midseason cohorts. Recruitment potential (*G*:*Z* ratio) was highest for midseason cohorts (1.30–1.56) and lowest for early and late-season cohorts (<1). Although *G*:*Z* ratios varied over spatial and temporal scales, ratios were >1 in 1994 and 1995, suggesting that both year classes experienced favorable nursery conditions.

Manuscript accepted 27 August 1998.
Fish. Bull. 97:581–590 (1999).

Survival during the larval and juvenile stages of marine fishes is highly variable and plays a critical role in determining recruitment potential (Cushing, 1975; Houde, 1987). Early life survival is a function of both growth and mortality, and it is clear that these mechanisms act in concert to determine an individual's probability of survival (Houde, 1996). Individuals experiencing rapid growth will spend less time in vulnerable size ranges (reduced stage duration) and achieve a larger body size at a given age, thus enhancing their ability to detect and escape predators (Bailey and Houde, 1989; Fuiman and Magurran, 1994). Consequently, recruitment success or failure is closely linked to variation in growth and mortality during the early life stage.

Much of our current understanding of early life growth and mortality is based on information derived from the examination of otolith microstructures. The daily deposition of growth increments on otoliths has been demonstrated for many marine teleosts and provides a means of estimating age, growth rate, and hatching date (see reviews by Campana and Neilson, 1985; Jones, 1986). Moreover, knowledge of a population's age structure can be combined with density data (abundance-at-age relationships) to estimate mortality rates. Thus, fundamental demographic parameters can be obtained through otolith analysis, and these data are essential for determining the causes and consequences of differential survival.

Red drum (*Sciaenops ocellatus*) inhabit subtropical and temperate waters in the Western Atlantic and support important commercial and recreational fisheries throughout the coastal waters of the Gulf of Mexico (Swingle, 1990; NOAA, 1991). Red drum spawn in the early fall in offshore waters and areas near tidal inlets, and tidal currents transport larvae through passes and into estuarine nursery habitats (Holt et al., 1989; Comyns et al., 1991). Individuals settle into sea-

* Contribution 1060 of Marine Science Institute, The University of Texas at Austin, Port Aransas, TX 78373.

grass and marsh-edge habitats following a fairly short pelagic interval and remain in these habitats during the juvenile stage (Baltz et al., 1993; Rooker and Holt, 1997; Rooker et al., 1998b).

Although much effort has been directed toward the management of red drum stocks, research on growth and survival during early life has received limited attention. As a result, the aim of this study was to examine spatial and temporal patterns of growth and mortality during the postsettlement period. Specific objectives of this research were to estimate annual variation in growth and mortality, to estimate cohort- and site-specific mortality rates, and to determine the recruitment potential of different cohorts.

Materials and methods

Field collections

Red drum were collected from two shoal grass (*Halodule wrightii*) meadows in the Aransas Estuary, Texas (Aransas Bay 1 and 2 [AB1, AB2]; Fig. 1), during the annual settlement period (August–December). Collections were taken over a two-year period (1994–95) with an epibenthic sled measuring 0.75 (w) × 0.5 (h) m, equipped with a 505-μm mesh conical plankton net. Triplicate 20-m sled tows were taken every week at each site in 1994. A more comprehensive sampling strategy was employed in 1995 in order to evaluate cohort-specific variation in natural mortality. Ten 20-m sled tows were taken every 3–4 d at each site during the entire 1995 settlement season. Red drum larvae and juveniles were preserved in 70% ethanol immediately after capture. Environmental data collected at each site included depth, salinity, and water temperature.

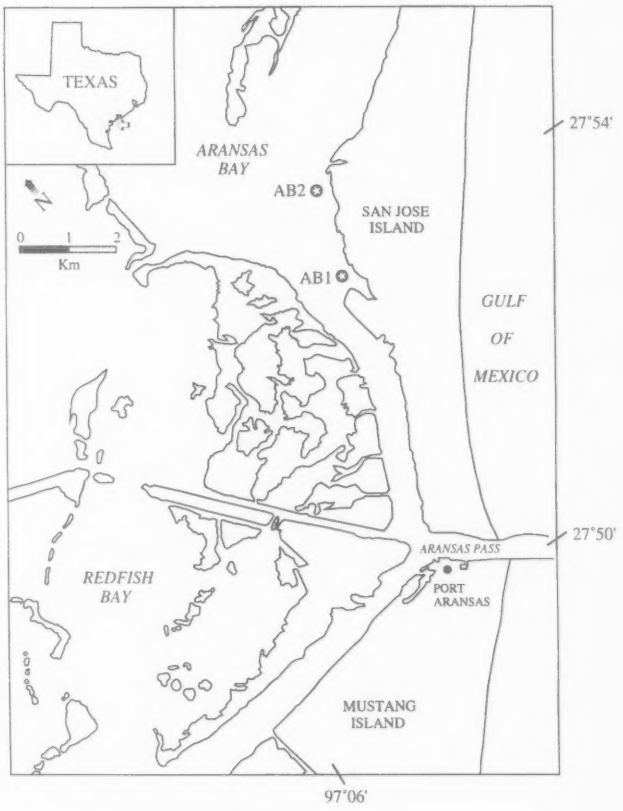


Figure 1
Location of shoal grass (*Halodule wrightii*) sampling stations (AB1 and AB2) in the Aransas Estuary, Texas.

Laboratory procedures

Removal and processing of otoliths (lapilli) followed the procedures described by Rooker and Holt (1997). Otolith radius, increment count, and increment widths were measured on a straight line from the core to the posterior edge using an image analysis system (Optimas, Bioscan). Because otolith growth is allometric (Campana and Neilson, 1985), all measurements were taken in the same field. Daily deposition of increments was validated in our laboratory by chemically marking the otoliths of known-age red drum with alizarin complexone (S.A. Holt, unpubl. data).

Age was determined by enumerating growth increments from the core to the margin of the otolith. Inner increments (proximal to the core) on lapilli were often difficult to enumerate. Thus, in order to accurately determine the age of wild red drum, a relationship between age and otolith radius from laboratory-reared red drum was developed and used to predict the number of growth increments at various distances from the core (Rooker and Holt, 1997). Age was determined by adding the predicted age from the unreadable section (correction factor from age-radius relationship) to the increment count (number of increments from first identifiable increment to edge of the lapillus). Correction factors generally accounted for less than 25% of the actual age estimate, and the relative size of the correction did not differ between years. Both the left and right lapilli were examined and estimates of age and growth were derived by averaging readings from both otoliths. On average, age differences between otoliths were small (CV=3.6%: range 0–14%). For some individuals

(18%), only one of the lapilli was available owing to loss, breakage, or staining.

Growth rates were determined by using otolith-derived estimates of age (size-at-age plots) in 1994 (n=249) and 1995 (n=140). Daily instantaneous growth coefficients were calculated from an exponential model described as

$$L_t = L_0 e^{gt},$$

where L_t = length (mm SL) at time t;
L_0 = the estimated length at hatching;
g = the instantaneous growth coefficient (/d); and
t = the otolith-derived age (days after hatching).

Ages of red drum not assessed with otolith-based techniques (1994 [n=1,057], 1995 [n=8004]) were estimated by using age-length relationships.

Weight-specific instantaneous growth coefficients (G) were calculated by using the equation

$$W_t = W_0 e^{Gt},$$

where W_t = the wet weight (mg) at time t;
W_0 = the estimated weight at hatching;
G = the weight-specific instantaneous growth coefficient (/d); and
t = the otolith-derived age.

Red drum lengths (mm) were converted to wet weight (mg) by using a polynomial equation (third order) based on measurements from laboratory-reared red drum (range: 6–30 mm): $W = -7.745 + 2.122L - 0.205L^2 + 0.024L^3$ (n=200, r^2=0.97), where W and L represent wet weight and standard length, respectively.

Mortality rates were estimated from regressions of the decline in $\log_e$-transformed abundance on age. Although interannual variation in mortality was examined by pooling individuals from each year (all cohorts combined), cohort-specific rates were based on regression plots of $\log_e$-transformed abundance of individuals from 10-d cohorts determined from hatching-date analysis. Hatch dates of individual red drum were determined by subtracting the otolith-derived age from the date of collection. Hatching dates were then used to separate individuals into specific cohorts, defined as individuals hatched within a 10-d period. Each cohort was designated by a letter (A to F): 1–10 Sep (A); 11–20 Sep (B); 21–30 Sep (C); 1–10 Oct (D); 11–20 Oct (E); and 21–30 Oct (F). Densities for the first and last cohort (A, F) were low and thus mortality regressions were not fitted to these data. Daily instantaneous mortality rates were calculated from the exponential model of decline:

$$N_t = N_0 e^{-Zt},$$

where N_t = abundance at time t;
N_0 = the estimated abundance at hatching;
Z = the instantaneous mortality coefficient (/d); and
t = the otolith-derived age.

Owing to incomplete capture (i.e. ascending limb of catch curve) of small red drum (<25 d, ≤8 mm), these individuals were not included in mortality regressions. Also, size-based gear avoidance was suspected, which placed constraints on the upper age (or size) of individuals used in regression analysis. In preliminary trials, the capture efficiency of the epibenthic sled was compared with a bag seine (seine dimensions: 7 m length × 1 m height; mesh size: 3 mm) and size-specific differences in capture efficiency (individuals/m^2 of habitat sampled) between the two gears were not detected for sciaenids <25 mm (Rooker, 1997). However, density estimates of sciaenids >25 mm were higher with the seine. This suggested that individuals >25 mm are capable of avoiding the sled and that densities calculated for these individuals would be underestimated. Consequently, only red drum between 8 and 20 mm (25–40 d) were used to estimate mortality rates.

Our assessment of early life mortality was based on two assumptions: 1) individuals entering seagrass sites remained in these habitats (i.e. settle and stay) during the time period when mortality rates were estimated, and 2) immigration and settlement (i.e. late settlers) to the designated study sites from other locations or habitats, or both, was negligible. Although postsettlement movement (emigration or immigration, or both) can be important for certain species and failure to account for such movements can severely bias mortality estimates (Frederick, 1997), our assumptions are reasonable because red drum appear to settle and stay in seagrass meadows at least through the early juvenile stage (Rooker et al., 1998b). Furthermore, no salient increases or decreases in density were observed in length-frequency profiles which would be expected in the presence of postsettlement emigration or immigration activity.

Since total mortality (Z) is the sum of both natural (M) and fishing mortality (F), it is important to account for the fishing mortality (F) caused by our sampling (Ricker, 1975). Most studies evaluating early life mortality do not estimate F (=sampling mortality) and assume F to be inconsequential. In this study, seagrass meadows of limited size (ca. 25,000 m^2) were sampled repeatedly and, as a result, the effect of F was considered potentially significant. Therefore, mortality regressions were run on abundance data

adjusted to compensate for sampling losses (F). Abundance at each sampling time was adjusted by subtracting the number of individuals collected (removed from population) with the epibenthic sled from the overall abundance at the site (site abundance = area of site/area sampled × number of red drum collected). Regressions of $\log_e$-adjusted abundance on age were then run and mortality coefficients derived in this manner were basically estimates of M since the effect of F was removed. Consequently, F was determined by subtracting adjusted mortality rate (M) from Z. Because F values were relatively small, 2.3 to 6.9% of Z, only estimates of Z are presented.

The relative recruitment potential of individual cohorts was assessed by examining the ratio of weight-specific growth (G) to mortality (Z). The ratio is commonly used as an index of stage-specific survival because it incorporates both growth and mortality (Werner and Gilliam, 1984; Houde, 1996). Because cohorts with G:Z ratios >1 gain biomass, the probability of survival (recruitment potential) for these individuals is assumed to be high.

Data analysis

Analysis of covariance (ANCOVA) was used to test for intra- and interannual differences in growth and mortality (covariate: age). Prior to each ANCOVA test, a preliminary model (interaction regression) was tested to determine if the slopes of the regression lines differed (homogeneity of slopes assumption; Sokal and Rohlf, 1981). The main significance test of the ANCOVA (homogeneity of y-intercepts) was performed when the parallelism of slopes assumption was met. Since differences in abundance affect the elevation of regression plots used to estimate mortality, spatial and temporal trends in mortality were evaluated by comparing slopes (y-intercept test not performed). Analysis of variance (ANOVA) was used to examine variability in density. Estimates of density were $\log_e$-transformed to minimize heteroscedasticity.

Results

Environmental conditions

Water temperature and salinity were recorded daily from August to December in 1994 and 1995. Temporal variation in both parameters was pronounced and trends were similar between years (Fig. 2). Temperature during the primary settlement period was variable (September–October) and ranged from 23.3° to 30.2°C in 1994 and from 22.7° to 31.6°C in 1995, respectively. Mean temperature during this period was similar between years 1995 (27.5°C) and 1994 (27.2°C). Salinity ranged from 25.3‰ to 37.0‰ and from 25.3‰ to 30.8‰ in 1994 and 1995, respectively. Similar to temperature, mean salinity was relatively similar between years: 30.0‰ (1994) and 28.6‰ (1995). Peak values for both parameters occurred during the initial spawning period and declined for later spawning and settlement dates. Cohorts arriving early in the season experienced high temperature and salinity, whereas late-season cohorts were exposed to lower temperature and salinity (Fig. 2). No conspicuous differences in temperature or salinity were observed between sampling sites (AB1, AB2).

Catch characteristics

Overall, 1306 and 8144 red drum larvae and early juveniles (3–40 mm) were collected from the two sampling sites in the Aransas Estuary in 1994 and 1995. In both years, settlers were first detected in early September and peak densities of recently settled red drum (≤10 mm) were present in early October (Fig 3). Larger postsettlers (>10 mm) were most abundant from mid-October to early November. Mean densities of recently settled red drum (<10 mm) ranged from 0.0 to 1.7/m^2 in 1994 and from 0.0 to 4.1/m^2 in 1995; densities of all postsettlement red drum (≤40 mm) ranged from 0.0 to 3.0/m^2 in 1994 and from 0.0 to 4.2/m^2 in 1995 (Fig. 3). Maximum densities (per sled tow) observed in 1994 and 1995 in the Aransas Estuary were 3.4/m^2 and 11.5/m^2, respectively. Interannual variation in postsettlement density during the two seasons (October–November) was small: 1.53/m^2 (1994), 1.63/m^2 (1995). No significant differences in density were detected between years or sites (ANOVA, P>0.05).

Although collection effort varied between years, length-frequency distributions of red drum from the Aransas Estuary were similar (Fig. 4). In both years, the smallest individuals collected were 3 mm and large recruits (>30 mm) were collected infrequently. Catch rates showed a steeply ascending left limb which peaked at approximately 8–9 mm, suggesting that recruitment to seagrass meadows was complete for these individuals. A long descending right limb characterized catches for individuals >10 mm.

Age and growth

Age-length relationships (age-length keys) were developed for each year class and described by the following equations: $Age = -17.05 + 42.25\ \mathrm{Log}SL$ (1994, n=249, r^2=0.90, CV=8.9); $Age = -11.43 + 40.11\ \mathrm{Log}SL$ (1995, n=140, r^2=0.90, CV=7.5). Predicted ages of red drum (3–30 mm) ranged from 6 to 45 d in 1994 and from 10

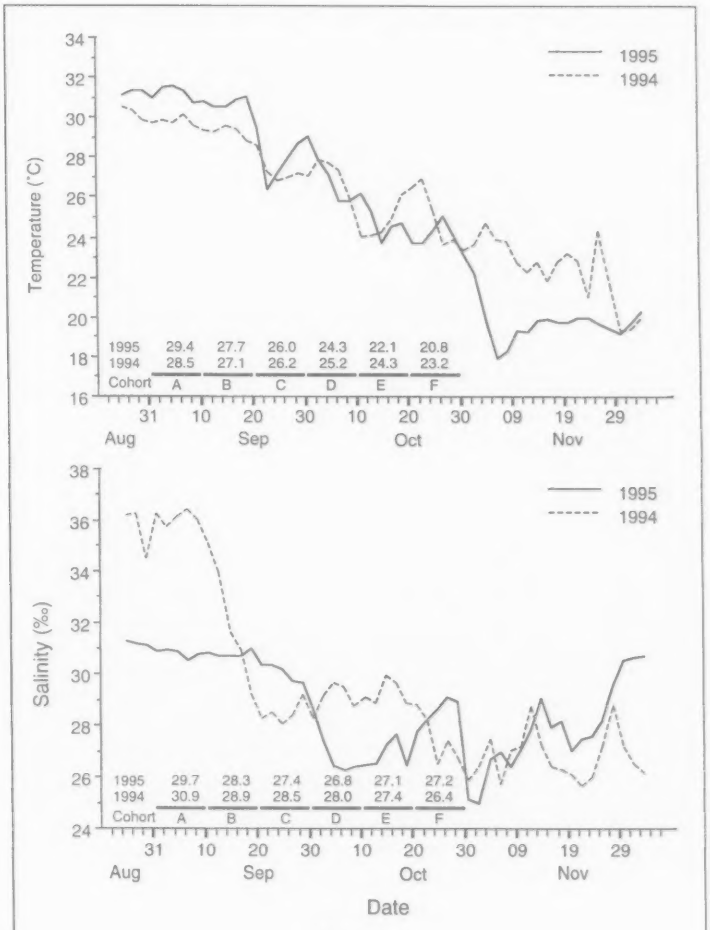


Figure 2

Water temperature and salinity records for the Aransas Estuary in 1994 and 1995. Mean temperature and salinity (30-d average) experienced by red drum cohorts (A–F) are given.

to 48 d in 1995. Individuals from the most abundant size class (8–10 mm) were approximately 20–28 d. Age data were used to determine hatch dates and these data were used to partition individuals into 10-d cohorts.

Instantaneous growth coefficients (g) ranged from 0.049 (4.8%/d) in 1994 to 0.051 (5.0%/d) in 1995 (Fig. 5) and differed significantly between years (ANCOVA, *y*-intercepts, $P<0.001$). Instantaneous growth coefficients were also estimated on a site-specific basis within the Aransas Estuary (Table 1). In 1994, growth rates at AB1 were significantly higher than AB2 (ANCOVA, *y*-intercepts, $P=0.015$); however, no site effect was observed in 1995 (ANCOVA, *y*-intercepts, $P=0.440$). The weight-specific growth coefficients (G) ranged from 0.159 to 0.162 (14.7–15.0%/d) and from 0.163 to 0.165 (15.0–15.2%/d) in 1994 and 1995, respectively (Table 1).

Mortality

Instantaneous mortality coefficients (Z) ranged from 0.134 (12.5%/d) in 1994 to 0.139 (13.0%/d) in 1995 and no significant interannual effect was observed (ANCOVA, slopes, $P=0.737$) (Fig. 6). Stage-specific mortality rates (cumulative mortality during the early postsettlement period: 12-d period, ca. 10–20 mm) ranged from 1.668 (81.1%) to 1.608 (79.9%) in 1994 and 1995, respectively. Spatial variation in mortality was also examined within each year by estimating mortality rates at the two sites within

the Aransas Estuary. Site-specific mortality rates in 1994 ranged from 0.129 to 0.141 and no significant difference was detected between sites (ANCOVA, slopes, P=0.741); however, in 1995 mortality rates were significantly lower in AB1 (0.129) than in AB2 (0.193) (ANCOVA, slopes, P=<0.001).

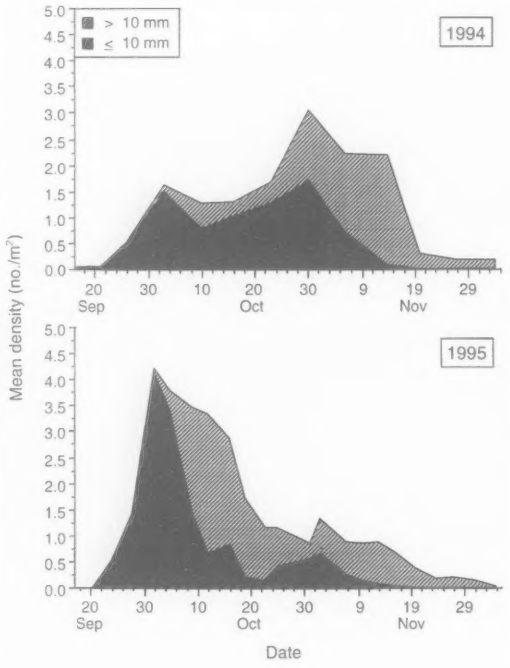


Figure 3

Mean density (sites pooled) per sampling trip of postsettlement red drum collected from the Aransas Estuary in 1994 and 1995. Two size classes of postsettlement red drum (≤10 mm SL, >10 mm SL) are shown.

Table 1

Growth and mortality coefficients of postsettlement red drum collected from the Aransas Estuary in 1994 and 1995. The *G:Z* recruitment index is also shown.

Year	Site	g	*G*	*Z*	*G:Z*
1994	AB1	0.051	0.159	0.141	1.128
	AB2	0.048	0.161	0.129	1.248
	All sites	0.049	0.162	0.134	1.209
1995	AB1	0.052	0.165	0.129	1.279
	AB2	0.049	0.163	0.193	0.845
	All sites	0.051	0.165	0.139	1.187

Cohort-specific mortality rates were estimated for the 1995 year class (Fig. 7). Instantaneous mortality coefficients for 10-d cohorts ranged from 0.106 (10.1%/d) to 0.265 (23.3%/d) and a significant temporal trend was detected (ANCOVA, slopes, P=0.004). Mortality rates were lowest for midseason cohorts (C, D) and highest for early and late cohorts (B, E), and individuals from the last cohort (E) experienced the greatest mortality. Stage-specific mortality rates (10–20 mm, 12 d) ranged from 1.272 to 1.524 (71.9–78.2%) for midseason cohorts and 2.316 and 3.180 (90.1–95.8%) for early and late-season cohorts.

G:Z Index

Recruitment potential of different cohorts was evaluated by comparing *G:Z* ratios and temporal variation was observed (Fig. 8). The ratio of *G:Z* was highest for mid-season cohorts; 1.305 (cohort C) and 1.565 (cohort D). In contrast, *G:Z* ratios of early and late-season cohorts (B, E) were <1, suggesting that these cohorts were losing biomass. Moreover, annual estimates of *G:Z* were calculated and ratios were >1 in both 1994 and 1995. Site-specific variation was also observed and, apart from site AB2 in 1995, *G:Z* ratios were always >1 (Table 1).

Discussion

Otolith-derived estimates of age indicate that red drum enter estuarine seagrass meadows after a short pelagic interval. Peak densities were observed for individuals 8–9 mm (20–24 d), suggesting that recruitment to seagrass meadows follows a planktonic period of approximately 20 d. In support of this finding, studies examining red drum during the planktonic phase have shown that the upper size range of red drum larvae in pelagic environments is 6–8 mm (Peters and McMichael, 1987; Comyns et al., 1989; Holt et al., 1989). In addition, Peters and McMichael (1987) sampled demersal habitats in Tampa Bay, Florida, and reported that red drum were first detected at 8 mm. Consequently, red drum appear to move from pelagic to demersal habitats (i.e. settlement) at approximately 8 mm.

Once in seagrass meadows, length- and weight-specific growth of red drum increases rapidly with increasing size (exponential relationships). Length-specific growth rates of new settlers (20–40 d) in the Aransas Estuary averaged 0.58 and 0.62 mm/d in 1994 and 1995, respectively. Growth estimates in the Aransas Estuary are similar to rates reported by Peters and McMichael (1987) for red drum in Tampa Bay, Florida (0.58 mm/d). With size-at-age equations

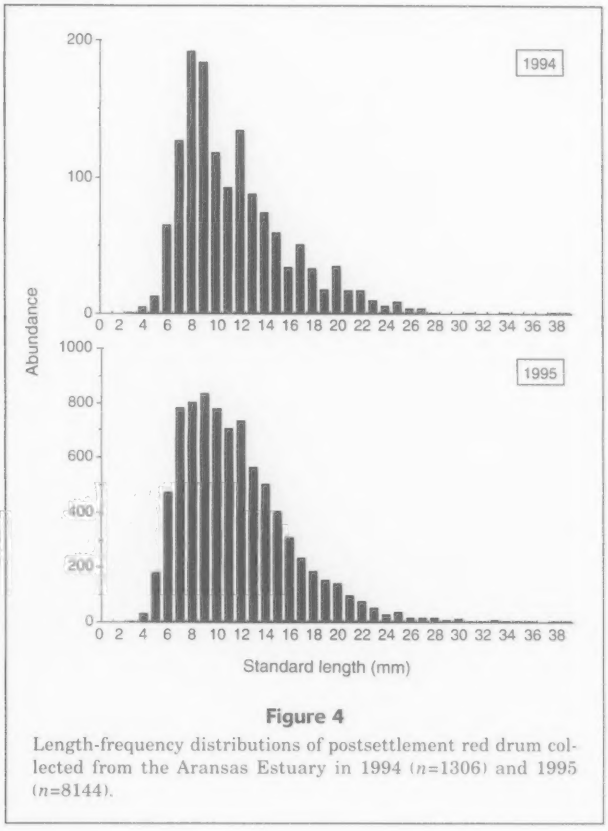


Figure 4

Length-frequency distributions of postsettlement red drum collected from the Aransas Estuary in 1994 (n=1306) and 1995 (n=8144).

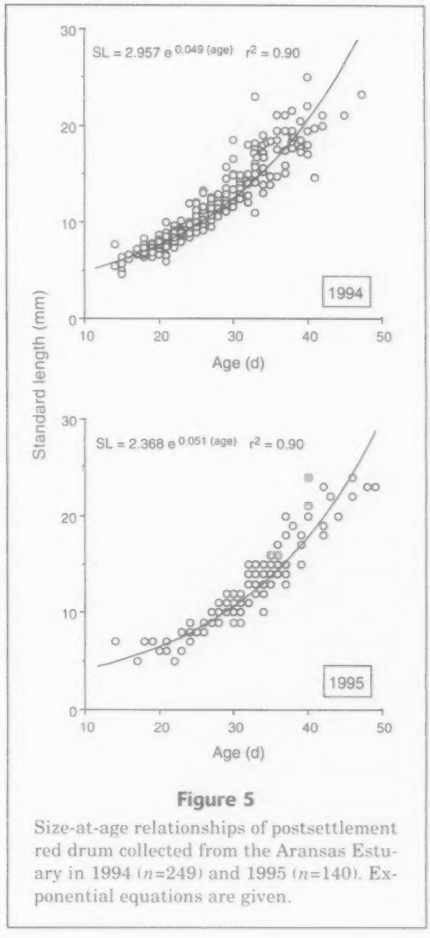


Figure 5

Size-at-age relationships of postsettlement red drum collected from the Aransas Estuary in 1994 (n=249) and 1995 (n=140). Exponential equations are given.

derived for red drum, we predicted that the length of a 40-d individual ranged from 20.2 mm (1994) to 18.2 mm (1995), which was similar to the predicted length of a 40-d individual collected in Tampa Bay (20.5 mm). Although seasonal trends in growth variation were not examined in this study, Rooker and Holt (1997) observed considerable variability among cohorts of newly settled red drum (0.5–0.8 mm/d), and growth was generally highest for midseason cohorts.

Mortality rates of red drum were substantial and varied over spatial and temporal scales. Interannual estimates of mortality were similar and losses ranged from 12.5 to 13.0%/d (Z=0.13–0.14). Consequently, cumulative mortality during the settlement and early postsettlement period (12-d period) was relatively high; only about 20% of the initial settlers survived to 40 d. Although no estimates of mortality exist for red drum larvae and early juveniles, these mortality rates are comparable to values reported for other marine fishes during the early life stage. Houde (1987) reported instantaneous daily mortality coefficients for five species of marine fishes during the larval stage (first feeding to late-stage larvae) and predicted values ranging from 0.04 to 0.18 (4–16%/d). In addition, Houde and Zastrow (1993) summarized natural mortality data for teleost larvae from a variety of sources and reported that the mean instantaneous daily mortality rate of larvae in estuarine habitats was 0.266 (23%/d). Also, McGurk (1986) developed a general mortality equation for marine fish larvae (based on dry weight), and using his equation we predicted the mortality rate of individual red drum 8–10 mm (ca. 750–1500 µg dry wt) would be approximately 0.05–0.11 (4.9–10.4%/d).

Although interannual patterns of mortality were insignificant, variability within a year was relatively high and a seasonal trend was evident. Cohort-specific estimates indicated that mortality rates were lowest for red drum produced in the middle of the spawning season (10%/d), when densities within the seagrass meadows reached maximum levels. Conversely, mortality rates for early and late-season co-

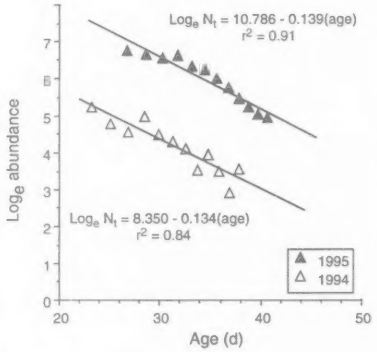


Figure 6

Regression plots of Log$_e$ abundance on age of postsettlement red drum collected from the Aransas Estuary in 1994 and 1995. Regression equations are given.

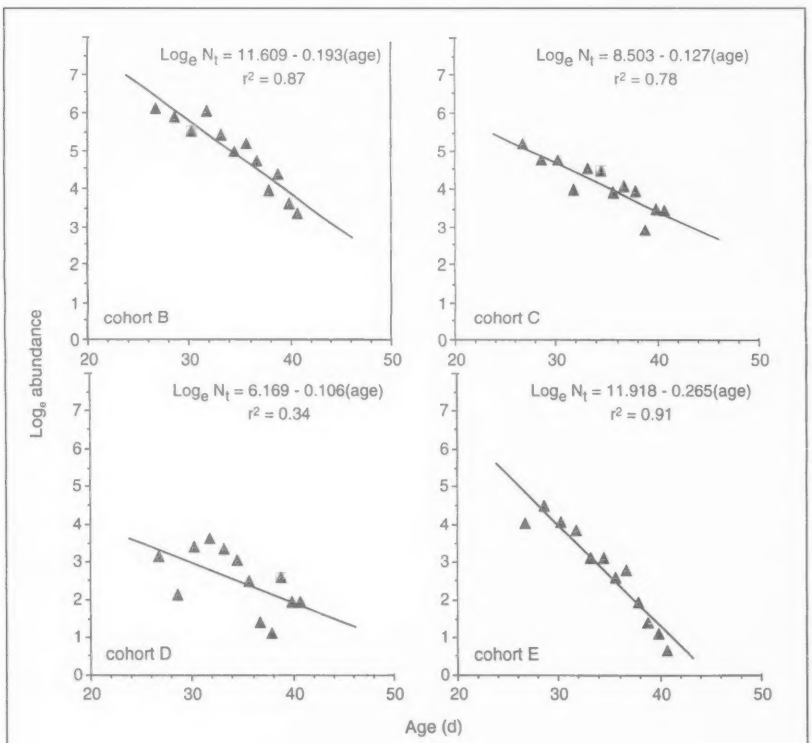


Figure 7

Regression plots of Log$_e$ abundance on age for 10-d cohorts of postsettlement red drum collected from one site (AB2) in the Aransas Estuary in 1995. Regression equations and plots are shown for cohorts B, C, D, and E.

horts were approximately twofold higher, approaching 25%/d for the late-season cohort. Seasonal fluctuations of this magnitude have been reported in several studies on marine fish larvae and attributed to changes in environmental conditions (e.g. temperature, prey availability) which can directly or indirectly influence mortality (Rutherford and Houde, 1995; Secor and Houde, 1995).

Temperature is often implicated as a critical factor in recruitment because it has the potential of influencing growth rates and causing episodic mortality during early life (Houde and Zastrow, 1993; Houde, 1996). Temperature has been shown to be a primary determinant of growth variation in laboratory and wild populations of red drum (Holt et al., 1981; Lee et al., 1984; Rooker et al., 1997). Moreover, Rooker and Holt (1997) determined that seasonal trends in growth variation for red drum were related to temperature. Mean temperatures experienced by successive cohorts declined throughout the season; however, growth rates were highest for mid-season cohorts (20 September–10 October) and lowest for early and late cohorts. Conversely, mortality rates were lowest for mid-season cohorts and highest for early and late cohorts. Growth and mortality data appear to be best described by curvilinear relationships (quadratic function), suggesting that there may be an optimal temperature range at which growth and survival of red drum are enhanced and that the midpoint of this range occurs at approximately 26°C.

Variability in other biotic and abiotic factors may also be responsible for observed trends in mortality. Similar to other marine fishes, growth and survival rates of red drum larvae are associated with prey availability (G.J. Holt, unpubl. data). Since spatial and temporal variation in prey density (i.e. meiofauna) are common in estuarine habitats in south Texas (Montagna and Kalke, 1992), seasonal trends in prey abundance may

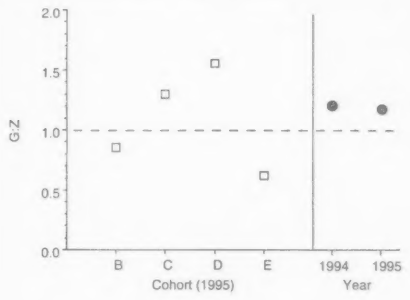


Figure 8

Recruitment potential (*G:Z* ratios) of 10-d cohorts of postsettlement red drum collected from the Aransas Estuary in 1995. Interannual estimates of *G:Z* are given.

have affected early life survival. Conversely, predator fields also vary spatially and temporally and survival may be a function of predator abundance. Postsettlement red drum are exposed to a suite of predators in the seagrass meadows and the abundance and distribution of these predators are highly variable (senior author's unpubl. data). Rooker et al. (1998a) examined predation rates on newly settled red drum in experimental mesocosms and demonstrated that predators inhabiting these seagrass meadows, are capable of consuming large numbers of red drum (Z=2–7%/[h · predator]). Consequently, fluctuations in prey and predator densities appear critical to the survival of red drum and the addition of this information to future studies should enhance our understanding of early life mortality.

Growth and mortality estimates were combined to evaluate the relative recruitment potential (*G:Z*) of red drum cohorts. According to Houde and Zastrow's (1993) review of 188 species, *G:Z* ratios for marine fish larvae are generally less than 1.0 (mean *G:Z*=0.89) and larvae inhabiting estuarine ecosystems tend to have low G:Z ratios (range: 0.34–0.82). However, recent work in Chesapeake Bay on striped bass (*Morone saxatilis*) has demonstrated that *G:Z* ratios can be >1 in estuarine ecosystems (Rutherford and Houde, 1995; Secor and Houde, 1995). Similarly, *G:Z* ratios for postsettlement red drum in the Aransas Estuary were >1 in both 1994 and 1995 (1.21 and 1.19, respectively) and, as a result, gross growth efficiency was positive and the recruitment potential of 1994 and 1995 year classes appears to have been favorable.

A high degree of correspondence in *G:Z* ratios between years was present, suggesting that conditions for growth and survival were similar in 1994 and 1995. Although the assessment of physical and biological conditions was limited (no data on prey availability or predator fields), parameters measured in this study (e.g. temperature, salinity, settlement size, and density) were relatively equal between years. In contrast, *G:Z* ratios of 10-d cohorts and the environmental conditions experienced by these individuals were highly variable within a single season. The *G:Z* ratios were highest (1.3–1.6) for midseason cohorts and settlement densities at these times were at maximum levels. Thus, it appears that physical and biological conditions in the seagrass meadows were optimal for growth or survival, or for both. The opposite trend was observed for individuals arriving early and late in the season. Because *G:Z* ratios of individuals from these cohorts were low (0.6–0.9), we postulated that nursery conditions experienced by early and late-season cohorts do not favor early life survival (low recruitment potential).

Acknowledgments

We thank Kathy Binney, Sharon Herzka, Patti Pickering, Cameron Pratt, and Andy Soto for providing assistance in the laboratory and field. The manuscript benefited from the comments of three anonymous reviewers. This work was supported by grants from the Texas Higher Education Coordinating Board Advanced Research Program (grant 003658-392), Texas A&M Sea Grant Program (grant NBR:RIF65), Sid W. Richardson Foundation, and fellowships to J.R.R (E.J. Lund, Julian C. Barton).

Literature cited

Bailey, K. M., and E. D. Houde
1989. Predation on egg and larvae of marine fishes and the recruitment problem. Adv. Mar. Biol. 25:1–83.

Baltz, D. M., C. Rakocinski, and J. W. Fleeger.
1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. Environ. Biol. Fish. 36:109–126.

Campana, S. E., and J. D Neilson
1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42:1014–1032.

Comyns, B. H., J. Lyczkowski-Shultz, D. L. Nieland, and C. A. Wilson.
1991. Reproduction of red drum, *Sciaenops ocellatus*, in the northcentral Gulf of Mexico: seasonality and spawner biomass. U.S. Dep. Commer., NOAA Tech Rep NMFS 95:17–26.

Comyns, B. H., J. Lyczkowski-Shultz, C. F. Rakocinski, and J. R. Steen Jr.
1989. Age and growth of red drum larvae in the north-central Gulf of Mexico. Trans. Am. Fish. Soc. 118:159–167.

Cushing, D. H.
1975. Marine ecology and fisheries. Cambridge Univ. Press, Cambridge, England, 278 p.

Frederick, J. L.
1997. Post-settlement movement of coral reef fishes and bias in survival estimates. Mar. Ecol. Prog. Ser. 150:65–74.

Fuiman, L. A., and A. E. Magurran.
1994. Development of predator defences in fishes. Rev. Fish. Biol. Fish. 4:145–183.

Holt, G. J., R. Godbout, and C. R. Arnold.
1981. Effects of temperature and salinity on egg hatching and larval survival of red drum, *Sciaenops ocellata*. Fish. Bull. 79:569–573.

Holt, S. A., G. J. Holt, and C. R. Arnold.
1989. Tidal stream transport of larval fishes into non-stratified estuaries. Rapp. P.V. Réun. Cons. Int. Explor. Mer 191:100–104.

Houde, E. D.
1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2: 17–29.
1996. Evaluating stage-specific survival during the early life of fish. *In* Y. Watanabe, Y. Yamashita, and Y. Oozeki (eds.), Survival strategies in early life stages of marine resources. AA Balkema, Rotterdam, p 51–66.

Houde, E. D., and C. E. Zastrow.
1993. Ecosystem- and taxon-specific dynamic and energetics properties of larval fish assemblages. Bull. Mar. Sci. 53:290–335.

Jones, C.
1986. Determining the age of larval fish with the otolith increment technique. Fish. Bull. 84:91–103.

Lee, W. Y., G. J. Holt, and C. R. Arnold.
1984. Growth of red drum larvae in the laboratory. Trans. Am. Fish. Soc. 113:243–246.

McGurk, M. D.
1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. Mar. Ecol. Prog. Ser. 34:227–242.

Montagna, P. A., and R. D. Kalke.
1992. The effect of freshwater inflow on meiofaunal and macrofaunal populations in the Guadalupe and Nueces Estuaries, Texas. Estuaries 15:307–326.

NOAA (National Oceanic and Atmospheric Administration).
1991. Our living oceans: First annual report on the status of U.S. living marine resources. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-F/SPO-1:47–48.

Peters, K. M., and R. H. McMichael Jr.
1987. Early life history of the red drum *Sciaenops ocellatus* (Pisces: Sciaenidae) in Tampa Bay, Florida. Estuaries 10:92–107.

Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

Rooker, J. R.
1997. Early life history of red drum (*Sciaenops ocellatus*) in subtropical seagrass meadows: patterns of condition, growth, and mortality. Ph.D. diss., Univ. Texas at Austin, Austin, TX, 192 p.

Rooker, J. R., and S. A. Holt.
1997. Utilization of subtropical seagrass meadows by newly settled red drum (*Sciaenops ocellatus*): patterns of distribution and growth. Mar. Ecol. Prog. Ser. 158:139–149.

Rooker, J. R., G. J. Holt, and S. A. Holt.
1997. Condition of larval and juvenile red drum (*Sciaenops ocellatus*) from estuarine nursery habitats. Mar. Biol. 127:387–394.

Rooker, J. R., G. J. Holt, and S. A. Holt.
1998a. Vulnerability of newly settled red drum (*Sciaenops ocellatus*) to predatory fish: is early survival enhanced by seagrass meadows? Mar. Biol. 131:145–151.

Rooker, J. R., S. A. Holt, M. A. Soto, and G. J. Holt.
1998b. Post-settlement patterns of habitat use by sciaenid fishes in subtropical seagrass meadows. Estuaries 21:315–324.

Rutherford, E. S., and E. D. Houde.
1995. The influence of temperature on cohort-specific growth, survival, and recruitment of striped bass, *Morone saxatilis*, larvae in Chesapeake Bay. Fish. Bull. 93:315–332.

Secor, D. H., and E. D. Houde.
1995. Temperature effects on the timing of striped bass egg production, larval viability, and recruitment potential in the Patuxent River (Chesapeake Bay). Estuaries 18:527–544.

Sokal, R. R., and F. J. Rohlf.
1981. Biometry, 2nd edition. W. H. Freeman, San Francisco, CA, 859 p.

Swingle, W. E.
1990. Status of the commercial and recreational fishery. *In* Red drum aquaculture, p. 22–24. Texas A&M Sea Grant Program report TAMU-SG-90-603, College Station, Texas.

Werner, E. E., and J. F. Gilliam.
1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15:393–425.

Estimation of sablefish, *Anoplopoma fimbria*, abundance off Alaska with an age-structured population model

Michael F. Sigler
Auke Bay Laboratory, Alaska Fisheries Science Center
11305 Glacier Hwy., Juneau, Alaska 99801-8626
E-mail address: Mike.Sigler@noaa.gov

Abstract.—Relative abundance of sablefish, *Anoplopoma fimbria*, in the waters off Alaska has been measured annually since 1979 with longline surveys. These extensive surveys provide precise measures of relative abundance. An age-structured model was fitted to the longline survey data to estimate absolute abundance. Estimates of recent exploitation rates for fully selected ages averaged 10%. Monte Carlo simulations of the age-structured model indicated that absolute abundance of Alaskan sablefish can be estimated reliably if age selectivity is asymptotic and not dome-shaped. Abundance estimates were reliable even when only length data and no age data were available. Dome-shaped selectivity gave biased and less precise estimates, probably owing to a parameter interaction between catchability and the shape of the selectivity function.

Manuscript accepted 18 August 1998.
Fish. Bull. 97:591–603 (1999).

Sablefish, *Anoplopoma fimbria*, is a long-lived species that inhabits the northeast Pacific Ocean and Bering Sea. This species supports a fishery in Alaskan waters, with catches ranging from about 10,000 to 35,000 metric tons (t) during the last two decades (Fig.1). The fishery mostly uses longline gear and primarily occurs on the upper continental slope, which is inhabited by adult sablefish (Fig. 2). Previously the fishery became compressed year-round during the mid-1980s to 10 days in some areas, until 1995, when management switched to individual fishing quotas and an eight-month season. The delay of the start of the season from 1 January to 1 April and later 15 May accompanied the compressed fishery season.

In Alaska, relative abundance of sablefish has been best measured by annual longline surveys since 1979. Longline surveys are preferred over trawl surveys for assessing sablefish because the longline surveys generally cover the areas that adult sablefish inhabit, namely the upper continental slope. The longline surveys have occurred between early May and late September. The survey and fishery generally take place in the same area, the upper continental slope but the fishery generally takes place over a narrower depth range. Trawl surveys have also been conducted in Alaska, but compared with the longline surveys, they have not sampled as deeply and have covered fewer years. In stock assessments for Alaskan sablefish prior to 1996 (Fujioka, 1995; Lowe, 1995), the limited trawl data were used to convert relative abundance from the longline survey to absolute abundance by calibration to the trawl (Rose, 1986), and the population was modeled by using a delay-difference analysis (Kimura, 1985). The formulation of the delay-difference analysis applied to Alaskan sablefish was modified to provide annual recruitment estimates, with the assumption that trawl surveys measure absolute abundance (Fujioka, 1995; Lowe, 1995). The Alaskan sablefish stock assessment was like other Alaskan groundfish stock assessments, which historically have assumed that trawl surveys measure absolute abundance (Alverson and Pereyra, 1969). This assumption probably is wrong because fish can escape under the net (Engås and Godø, 1989a) and be herded by the bridles (Engås and Godø, 1989b). The motivation for the current study was to assess Alaskan sablefish without this assumption, relying only on longline survey estimates of relative abundance.

In the current study, I estimated absolute abundance for Alaskan sablefish with an age-structured population model, evaluated the estimation approach with Monte Carlo simulations, and investigated interactions of model parameters. Delay-difference analyses use annual abundance estimates and catches, whereas age-structured analyses additionally use annual

age or length data. The additional information allows explicit tracking of cohorts, but many more parameters must be estimated.

Fitting population models to survey and fishery data has long been used to estimate absolute abundance (Pope and Shepherd, 1985; Deriso et al., 1985) and is one method of estimating absolute abundance along with direct surveys, mark-recapture experiments and depletion experiments. Abundance estimation with a population model works by tracking population additions and losses and inferring absolute abundance from the manner in which catch affects the survey index and age and length compositions. In simple terms and aside from other losses, if harvesting 500 individuals decreases a cohort's index 10%, then the cohort's initial abundance was 5000 individuals. Estimation depends on having an abundance index precise enough to detect cohort reductions by the fishery.

The population model presented here takes into account the following unusual attributes of the available data. Length compositions are available from the longline surveys for all years analyzed, compared with infrequently available age compositions (Table 1). Not many Alaska-wide sablefish fishery data are available, consisting only of total catches and five years of fishery lengths, but no ages (Table 1).

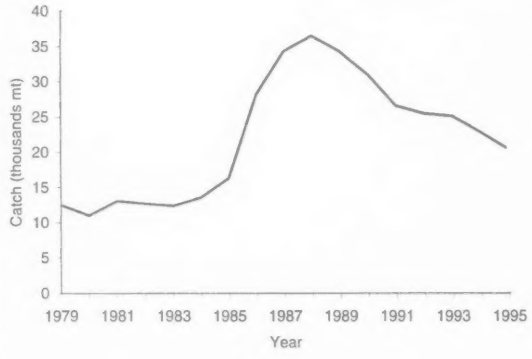


Figure 1

Reported fishery catches (thousands metric tons) from 1979 to 1995.

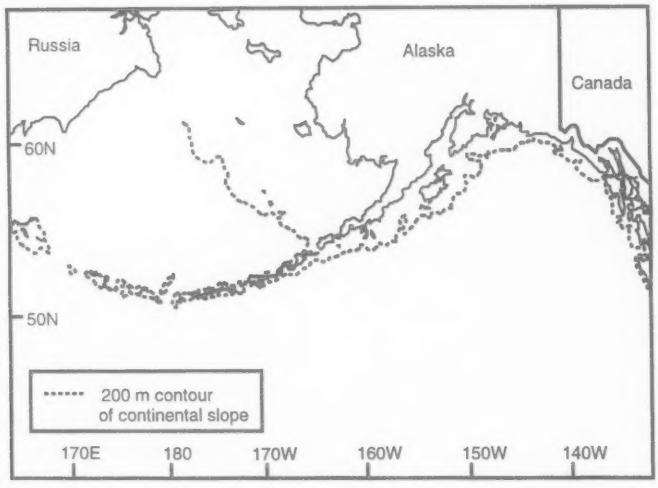


Figure 2

Map of southern Alaskan waters. Adult sablefish inhabit the upper continental slope seaward of the 200-m depth contour.

Methods

Model structure and estimation method

The analysis generally follows the approach described by Kimura (1990) for a separable age-structured population model. Let y, a, and l be the year, age, and length indices, respectively.

c_y = observed fishery catch in numbers;

I_y = observed survey abundance index in numbers;

p_{ya} = observed survey proportion at age;

p_{yl} = observed survey proportion at length;

$\mu_{ya} = \mu_y s_a$ = the exploitation fraction of age-a fish during year y which is separable into s_a, the selectivity for age-a fish, and μ_y, the exploitation fraction for fully vulnerable ages;

N_{ya} = the total number at age;

$N^f_{ya} = s_a N_{ya}$ = the exploitable (fishable) number at age; and

$\sum_a N^f_{ya} = N^f_y$ = the exploitable number.

Starting with initial cohort size, N_{ya}, natural deaths and observed catch were removed to compute next year's cohort size, $N_{y+1,a+1} = (1-\mu_{ya})\, N_{ya}\, e^{-M}$. A discrete fishery was modeled, $c_y = \mu_y N^f_y$, because the fishery was short for recent years except 1995. The modeled discrete fishery generally matches the timing of the observed discrete fishery and occurs near the mid-point of the earlier year-round fishery.

Table 1

Data sets used in the age-structured model of Alaskan sablefish. Length data are specified by sex.

Data component	Data aggregation	Years of data
Longline survey relative abundance	—	1979–95
Longline survey male lengths (cm FL)	40–41, 42–43, ..., 62–63, 64–69, 70–74, ..., 95–99	1979–95
Longline survey female lengths (cm FL)	40–41, 42–43, ..., 68–69, 70–74, 75–79, ..., 95–99	1979–95
Longline survey age	2, 3, 4, 5, 6, 7, 8, 9–10, 11–15, 16+ years	1983, 87, 89, 91, 93
Fishery total catch	—	1979–95

The modeled discrete fishery misrepresents the duration of the earlier year-round fishery, but tests with simulated data comparing a continuous fishery showed little difference in estimated abundance. The assumption of a discrete fishery simplified catch accounting and reduced model convergence time, which was important for the Monte Carlo simulations. This formulation limits the maximum exploitation rate for an age class to equal the selectivity for that age. This maximal rate would be achieved if the maximally selected age were completely harvested, with the exploitation rate equal to 1.0. This potential problem is not a real one because exploitation rates never approach such high levels for Alaskan sablefish.

Selectivity was described by the "exponential-logistic" function (Thompson, 1994),

$$s_a = \left(\frac{1}{1-\gamma}\right)\left(\frac{1-\gamma}{\gamma}\right)^{\gamma}\left(\frac{e^{\beta\gamma(A_{50}-a)}}{1+e^{\beta(A_{50}-a)}}\right).$$

The "exponential-logistic" function is flexible, allowing both asymptotic selectivity when selectivity increases with age to an asymptote, and dome-shaped selectivity when selectivity increases with age to a maximum, then decreases for older fish. The exponential-logistic function automatically scales maximum selectivity to 1.0 and reduces to asymptotic selectivity as the parameter gamma (γ) approaches zero. When $\gamma = 0$, the parameter A_{50} is the age where 50% of the population is vulnerable and β is the slope of the function at A_{50}. When $\gamma > 0$, then A_{50} and β lose their biological meaning, because A_{50} no longer represents the age at 50% vulnerability. Selectivity is assumed equal for the fishery and survey. Both the fishery and survey mostly use longline gear and cover the same area. Their similar length frequencies support this assumption (Fig. 3). The fishery length data were not incorporated into the model because of this similarity and because few years of fishery length data were available.

Age data were aggregated over adjacent ages (Table 1) as suggested by Deriso et al. (1989) because sablefish are difficult to age, especially those older than eight years (Table 6 in Kimura and Lyons, 1991). Ages greater than eight years were not pooled into a single class because females continue to grow, though slowly, after eight years. This growth information was needed in the model to convert ages to lengths. Length data also were aggregated (Table 1). Another way to deal with ageing error is to include a matrix of misageing probabilities in the age-structured model (Kimura, 1990), but this approach was not used because the misageing probabilities were unknown.

Estimated data values were computed from the parameter estimates. The estimated abundance index is $\hat{I}_y = \hat{q}\hat{N}^f_y$, where q is survey catchability. Quantities estimated from this model and used in the model fitting algorithm are denoted with "hats." The estimated age compositions are

$$\hat{p}_{ya} = \frac{\hat{N}^f_{ya}}{\sum_a \hat{N}^f_{ya}}.$$

An age-length transition matrix, $L = (l_{al})$, also was calculated from the survey age data, where l_{al} is the probability that a sampled fish of age a will be of length l. The age-length transition matrix is assumed constant over time. Probabilities were computed by region and year, then pooled as an average weighted by sample size. Estimated age compositions were converted to estimated length compositions with the age-length transition matrix,

$$\hat{p}_{yl} = \sum_a \hat{p}_{ya} l_{al}.$$

The parameters were estimated by maximum likelihood by assuming multinomial errors for age and length data and log-normal errors for catch data (Fournier and Archibald, 1982) and by using the quasi-Newton algorithm implemented in Microsoft Excel. Assuming that the effective sample sizes are the same for age and length samples and that the

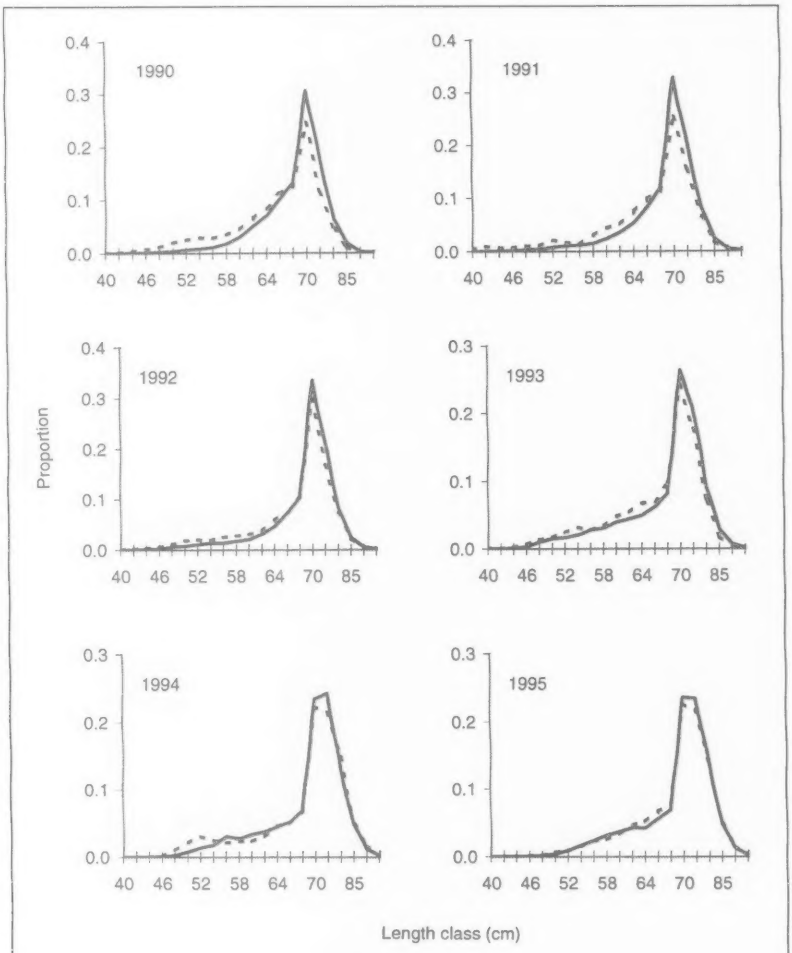


Figure 3

Survey (——) and fishery (– – –) length compositions for females. Male lengths also are available, but only female lengths are displayed for brevity. Alaska-wide fishery length data were available only since 1990.

age and length samples are independent, then the log-likelihood is

$$L = \sum_{ya} p_{ya} \log \frac{\hat{p}_{ya}}{p_{ya}} + \sum_{yl} p_{yl} \log \frac{\hat{p}_{yl}}{p_{yl}}$$
$$-\lambda \sum_{y} \left(\log(I_y) - \log(\hat{q}\hat{N}_y^f) \right)^2 + \text{constant},$$

where λ is the ratio of the effective multinomial sample sizes, either age or length, to the variance of the log-transformed abundance index (Deriso et al., 1985). Thus λ is a weighting factor that adjusts the relative influence of the abundance index and age and length components of the likelihood. The range of λ from 0.02 to 10 was tested. The value $\lambda = 1$ appeared the most reasonable and is used henceforth. This value was chosen on the basis of fit of each data type and the effect on the estimated recruitment values as λ was varied. As λ increased from 0.02 to 10, the fit of the index data improved only at the expense of the fit of the length data, but the relative sizes of the annual recruitment estimates were unaffected for $\lambda < 2$. Increasing λ substantially improved the fit of the index data until λ was from 1 to 2, when improvement slowed. Thus a value of λ between 1 and 2 seems reasonable, with $\lambda = 1$ chosen because the fit of the age data was best at that point. In prac-

tice, $\lambda = 1$ implies an effective sample size for the age and length samples of 100 if the CV of the survey index is 10%. This CV is reasonable according to a statistical analysis of the survey index, which found that a 10% interannual change in the survey index typically was statistically significant at the $P = 0.05$ level (Sigler and Fujioka, 1988). The reasonableness of the effective sample size is harder to determine because the age and length samples are composites of multinomial samples from survey stations with underlying geographic variation in age and length compositions, so that the effective sample size is less than the true sample size. In the above expression $\log(\hat{p}_{ya})$ usually found in the log-likelihood for the multinomial distribution was replaced with $\log(\hat{p}_{ya}/p_{ya})$. This replacement removes a "nonsignificant" portion of the likelihood and makes it easier to examine the model fit and probably somewhat improves numerical performance (Kimura, 1990).

Assuming M and λ are known, this model contains $Y + A + 2$ parameters: recruitment, $N_{11}, \ldots, N_{Y1}$, the initial age composition, $N\hat{q}_{12}, \ldots, N_{1A}$, and the selectivity parameters, A_{50}, β, and γ are unknown. The quantities and $\hat{\mu}_1, \ldots, \hat{\mu}_Y$ are functions of the observed survey indices and observed catches and of the parameter estimates. Setting dL/dq equal to zero and solving for q gives

$$\hat{q} = \exp\left[\frac{\sum_y \log \frac{I_y}{\hat{N}_y^f}}{Y}\right].$$

The $\hat{\mu}_1, \ldots, \hat{\mu}_Y$ are computed from $\hat{\mu}_y = \frac{c_y}{\hat{N}_y^f}$,

by treating reported catches as exact. Although clearly there will always be some error in the reported catch, I concluded that this approximation generally was reasonable given the comprehensive system for tracking the Alaskan sablefish catch, which includes processor reports, fish receipts, individual fishing quota landing reports, and observer coverage. I estimated log-parameters rather than parameters on the original scale to improve reliability in the estimation process (Kimura, 1989, 1990).

An allowable biological catch (ABC_{96}) was calculated from a 1-year future projection. The constant fishing mortality, $F_{40\%}$, was applied, which reduces the exploitable population to 40% of the unexploited state (Clark, 1991). A 1-year projection of recruitment was forecast as the average of recent estimated recruitments. The two most recent recruitments were not used in the average; their estimates, based on only one or two years of data, are unreliable.

Validation of estimation method

I used Monte Carlo simulation for model validation (Kimura, 1989; Press et al., 1989) to verify that the age-structured analysis provides reasonable results. The steps (Press et al., 1989) are as follows: 1) Fit the model using real data; 2) take the estimated parameter values as the true values for the simulation; 3) calculate the expected data based on these parameter values, then simulate a new data set by adding a particular error to the expected data based on an observed mean square error (MSE) or any hypothetical value; and 4) estimate the model parameters for the simulated data. If the resulting parameter estimates and the true parameter values are similar, then the estimation method is to some extent validated. This approach assumes that the model fits the simulated data perfectly except for random error. If the true errors were of larger magnitude or arose from a different source than that assumed in fitting the model, for example in violating the assumptions of equal fishery and survey selectivity and constant growth rates, then estimation performance with simulated data overstates the true model performance.

Log-normal error (CV=0.10 on the original scale) was added to the expected abundance index, and multinomial error (n=200) was added to the expected age and length data. These values were based on variability of the model residuals (difference between the observed and expected data). The log-transformed abundance indices are assumed to be independent, normally distributed random variables, and a "minor dilemma" (Kimura, 1989) arises on whether to simulate the abundance indices so that they are unbiased on the original or the logarithmic scale. I chose to simulate the abundance indices so that the survey index was unbiased on the original scale.

Age data are often limited in availability, whereas length data are nearly always available. Age data are more desirable than length data for estimating age structure because the correspondence between age and length is not one-to-one. Age data are commonly inaccurate: some individuals, especially older fish, are misassigned to ages around the true age. Thus, inaccurate age data and length data are similar in that true age does not uniquely correspond to assigned age or length. Parameters were estimated from simulated data for both accurate and inaccurate age data, the latter also being equivalent to length data. For accurate age data, 100% of fish of simulated samples were correctly assigned and cat-

egorized as {2, 3, ..., 15, 16+} . For inaccurate age or length data, 50% were correctly assigned to the true age, 20% to –1 year, 20% to +1 year, 5% to –2 years, and 5% to +2 years, then categorized as {2, 3, ..., 8, 9+} .

Survey selectivity may affect parameter estimation. Bence et al. (1993) found that biomass estimates were more accurate and precise for a population model with data from a survey with asymptotic selectivity than from one with dome-shaped selectivity. Therefore, both asymptotic and dome-shaped selectivity were compared. The dome-shape was chosen such that the availability of the last age group was 0.5.

A measure of the variability of biomass estimated in the simulations is the MSE computed from parameter estimates and their "true" values. Mean square error (MSE) was converted to coefficient of error (CE), defined as the "true" value divided into the square root of MSE (Kimura, 1990). Twenty-five to fifty replicate simulations were completed for each scenario.

Results

Model results for the original data

The model fitted all the original data well: abundance index (Fig. 4), age data (Fig. 5), and length data (Fig. 6). The estimate of survey catchability appears good; the likelihood profiled over a range of catchabilities shows a distinct, regular curvature (Fig. 7). Estimated exploitable biomass for 1995 was 181,000 t (Fig. 8), and projected ABC_{96} was 19,600 t. Estimated biomass decreased from a peak in the mid-1980s. The peak is attributed to strong recruitment in the late 1970s; recruitment has decreased in recent years (Fig. 9). Estimates of recent exploitation rates for fully selected ages average 10% (Fig. 8), which is near the exploitation rate equivalent to $F_{40\%}$, the current reference point for sablefish management in Alaska. The shape of the estimated selectivity curve was asymptotic (i.e. γ=0).

Figure 4

Observed (——) and expected (– – –) survey index (numbers) from 1979 to 1995.

The estimate of natural mortality for sablefish is uncertain; therefore its effect on abundance estimation was examined. An important part of this examination was to analyze the interaction between M and other key parameters. Model parameters were estimated for several fixed values of natural mortality around M = 0.10 (Table 2). The log-likelihood is not maximized at M = 0.10, and there is a slightly higher value for M = 0.12 (panel 1). Catchability was smaller and exploitable biomass was larger for larger M (panel 2); biomass was larger to account for more natural deaths. The fishable fraction of the total population

$$\left(\sum_a s_a N_{ya} \Big/ \sum_a N_{ya} \right)$$

was smaller for larger M (panel 3) because the fish recruited later (panel 4). Asymptotic selectivity was estimated whatever the value of M (panel 5). ABC_{96} was larger for larger M (panel 6) because exploitable biomass was larger and the fishing rate, $F_{40\%}$, increases with M.

Natural mortality and survey catchability can affect abundance estimates; therefore their effect was examined. Model parameters were estimated for several fixed values of q and M (Table 2). For each fixed M, the approach was to fix q at values near the estimated q. The results are likelihood profiles of q for each fixed M (panel 1). Given M, exploitable biomass was smaller for larger q (panel 2). The effect of q on the fishable fraction was more complicated. Given M, the fishable fraction was smaller for the fixed q that was less than the estimated q (panel 3) because older fish were less vulnerable to the fishery (panel 5). Given M, the fishable fraction was less for the fixed q that was greater than the estimated q because fish recruited later (panel 4). Selectivity was asymptotic and could not increase above 1.0, forcing the decreased fishable fraction to occur by means of a later recruitment age. ABC_{96} was larger for smaller values of q (panel 6) because exploitable biomass was larger (panel 2).

Model results for the simulated data

Biomass estimates were unbiased for simulations based on a survey with asymptotic selectivity, when

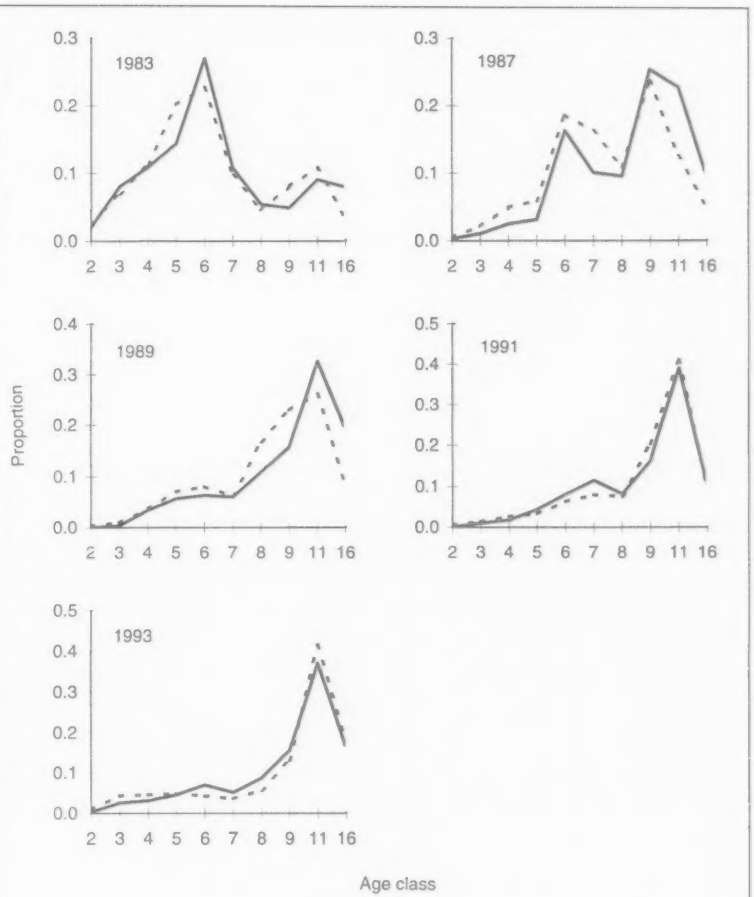


Figure 5

Observed (——) and expected (– – –) age compositions. Data were available only from the 1983, 1987, 1989, 1991, and 1993 surveys. See Table 1 for age-class definitions.

age and length data were used (Fig. 10A). Estimated error (CE [exploitable biomass]) was about 0.08, increasing for the later years to about 0.12 (Fig. 11), values similar to the assumed CV for the abundance index of 0.10. These values all imply that sablefish abundance could be estimated given the type and quality of data assumed in these simulations. These simulations match my evaluation of the actual data. Biomass estimates also were unbiased for asymptotic selectivity, no matter whether age or "length" data were used (Fig. 10, B and C); CE (exploitable biomass) ranged from 0.10 to 0.15 (Fig. 11). In contrast, biomass estimates were positively biased by 14% to 17% for dome-shaped selectivity (Fig. 10D) and CE (exploitable biomass) ranged from 0.40 to 0.50 (Fig. 11). Thus, estimating abundance from a survey with asymptotic selectivity appears reasonable; biomass estimates derived from a survey with dome-shaped selectivity can be estimated, but may be biased and less precise.

Discussion

Comparison of age-structured and delay-difference analyses

The estimates of sablefish exploitable biomass from age-structured analysis and delay-difference analysis are similar (Fig. 12). Both analyses show exploitable biomass rising from about 170,000 t in 1979, peaking at about 420,000 t around 1986, and falling since then to about 200,000 t in 1995. The trend from the sablefish delay-difference analysis is less smooth

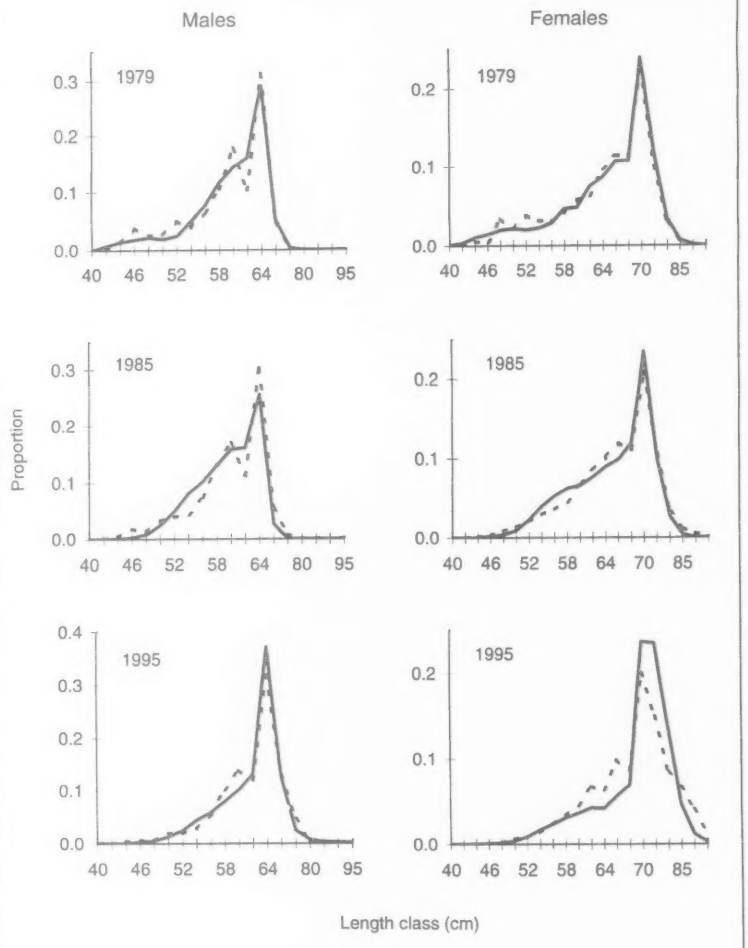


Figure 6

Observed (——) and expected (– – –) length compositions. Data were collected during all annual surveys from 1979 to 1995, but only a subset is displayed for brevity. See Table 1 for length-class definitions.

because the estimates are linear functions of the survey abundance index. Exploitable biomass follows every up and down in the abundance index. All measurement error is reflected in the recruitment estimate. The trend from the age-structured analysis is a complicated function of the abundance index and the age and length data and smooths annual changes in the abundance index.

The simulations in this paper imply that the age-structured model provides reliable estimates of sablefish absolute biomass. The assumption that trawl surveys provide absolute biomass estimates required for the sablefish delay-difference analysis can be dropped. Starting with the 1997 fishing year, the age-structured analysis has supplanted the delay-difference analysis in the stock assessment for estimating biomass(Fujioka et al., 1996).

Comparison to other estimates of sablefish abundance

Sablefish absolute abundance was estimated in two other studies, but the estimates were unreasonable. Sablefish longline catchability was estimated by depletion experiments (Clausen et al., 1997). The computed longline catchabilities were applied to the sablefish longline survey results for the Gulf of Alaska; the resultant biomass estimates of 50,000–

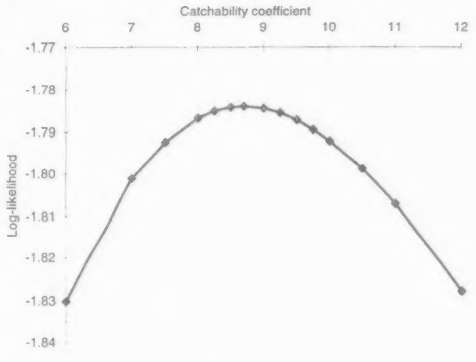


Figure 7
Log-likelihood versus catchability coefficient.

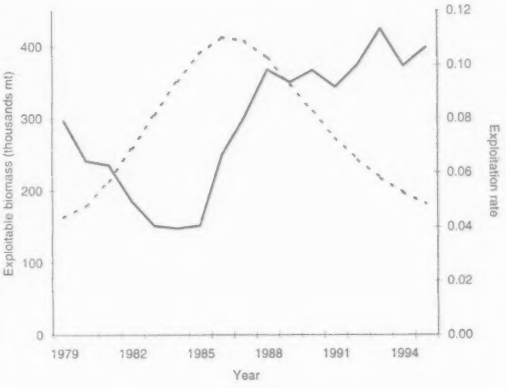


Figure 8
Estimated exploitable biomass (– – – , thousands metric tons) and exploitation rate (——) versus year.

60,000 t were unreasonably low because during the same period, the longline relative abundance index was stable even though annual commercial catches were 20,000–30,000 t (Clausen et al., 1997).

Eggers et al. (1982) described a quantitative method of estimating the effective radius of a baited hook or pot by comparing catch rates between gear with different spacings between baits. They applied this method to a hook-spacing experiment for sablefish longline gear and estimated that the bottom area fished per hook was 4.8 m^2. I applied this estimate to the time series of longline relative abundance indices, which implied that sablefish absolute biomass in Alaska ranged from 7 to 16 million t during 1979 to 1996, a range that seems improbably high because catches of about 50,000 t in the early 1970s subse-

Table 2

Log-likelihood, estimated values of exploitable biomass (thousands metric tons, age 2+) for 1995, the fishable fraction of the total population in numbers for 1995, age at 50% vulnerability, vulnerability of the last age class (s_{term}, where $s_{term} < 1$ implies a dome-shaped selectivity function), and projected allowable biological catch for 1996 (ABC_{96}). Values were estimated from the original data. Log-likelihood is the value of the objective function. Selectivity, recruitment, and initial age composition always were estimated. Asterisk (*) indicates results where survey catchability was estimated and natural mortality was fixed. No * indicates results where survey catchability and natural mortality were fixed.

Catchability coefficient	Natural mortality (M)				
q	0.05	0.08	0.10	0.12	0.15
Log-likelihood					
4.17				−1.781	−1.757*
6.85			−1.795	−1.770*	−1.789
8.70		−1.817	−1.784*	−1.786	
10.61	−1.869	−1.802*	−1.801		
13.59	−1.834*	−1.837			
Exploitable biomass					
4.17				366	362*
6.85		229	226*	215	
8.70		184	181*	175	
10.61	152	151*	146		
13.59	121*	115			
Fishable fraction					
4.17				0.735	0.821*
6.85			0.770	0.826*	0.789
8.70		0.772	0.830*	0.806	
10.61	0.673	0.833*	0.809		
13.59	0.837*	0.801			
Age at 50% availability					
4.17				4.0	4.2*
6.85			4.0	4.1*	4.6
8.70		3.9	4.0*	4.4	
10.61	4.0	4.0*	4.3		
13.59	3.9*	4.5			
s_{term}					
4.17				0.70	1.00*
6.85			0.78	1.00*	1.00
8.70		0.78	1.00*	1.00	
10.61	0.52	1.00*	1.00		
13.59	1.00*	1.00			
ABC_{96}					
4.17				68.5	62.9*
6.85			33.4	30.2*	39.0
8.70		22.7	19.6*	24.0	
10.61	23.0	12.8*	16.2		
13.59	6.4*	10.1			

quently resulted in sharp declines in fishery catch rate (Fujioka, 1986; McDevitt, 1986).

An estimate of the area occupied by adult sablefish was used to calculate the depletion and hook-spacing estimates of absolute biomass. The estimated area is inexact and, correspondingly, so are these biomass estimates. However this area would have to be an order of magnitude higher or lower to be consistent with the observed catch effects on the abundance indices, a level of error unlikely given the extensive longline surveys for sablefish.

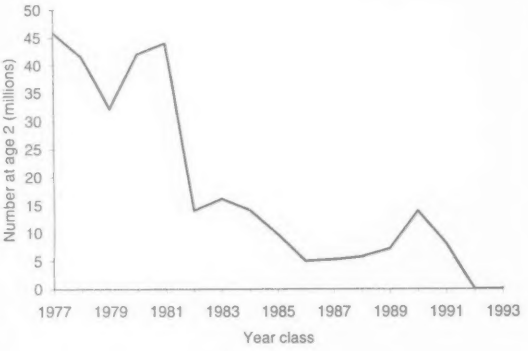


Figure 9
Number at age 2 (millions) versus year class.

Data and model requirements necessary to estimate abundance

Estimates of absolute abundance for sablefish were unbiased (Fig. 10, A–C) and relatively precise (Fig. 11) when selectivity was asymptotic. Abundance estimates were relatively precise regardless of whether age data alone, length data alone, or age and length data together were used. Even though length data alone is less desirable than age data for estimating annual recruitment, the precision of the abundance estimates was similar, supporting the notion that length data is useful for abundance estimation with age-structured analyses.

Dome-shaped selectivity affects abundance estimation. Sablefish abundance estimates were positively biased (Fig. 10D) and less precise (Fig. 11) for a survey with dome-shaped selectivity. Abundance estimates for a simulated widow rockfish, *Sebastes entomelas*, fishery off the western coast of the continental United States also were less accurate and less precise for a survey with dome-shaped selectivity than one with asymptotic selectivity (Bence et al., 1993). Thus, surveys with asymptotic selectivity appear better for abundance estimation than surveys with dome-shaped selectivity.

The sablefish age-structured model was fitted with 17 years of survey length data, but only five years of survey age data and no fishery age or length data. Two assumptions probably were the keys to how it was possible to fit an age-structured model with only limited age data (Table 1). One key assumption is that selectivity is equal for the fishery and survey, so that no fishery age or length data were required to independently estimate fishery selectivity. Another key assumption is that the age-length transition matrix is constant over time, so that

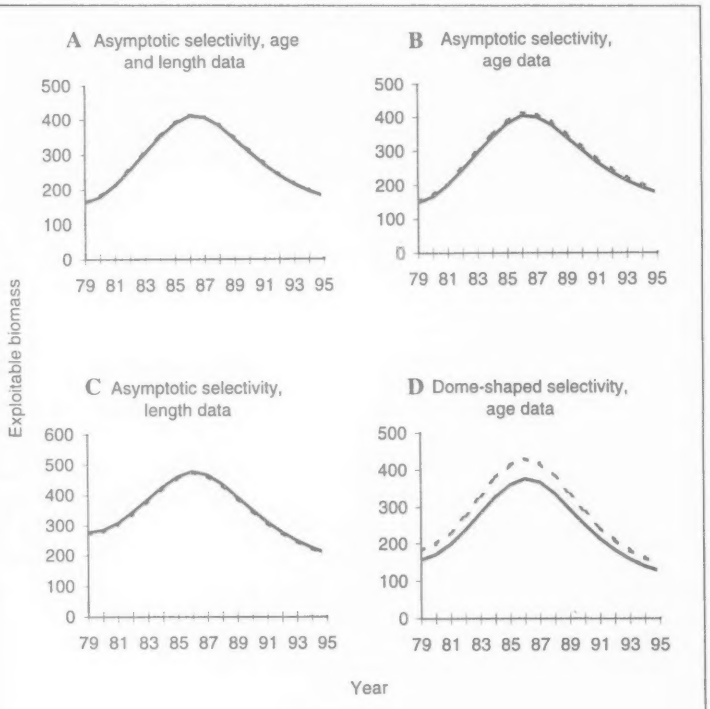


Figure 10
Exploitable biomass (thousands metric tons) versus year for simulated data. The "true" values (——) are compared with the average values (– – –) for the simulations.

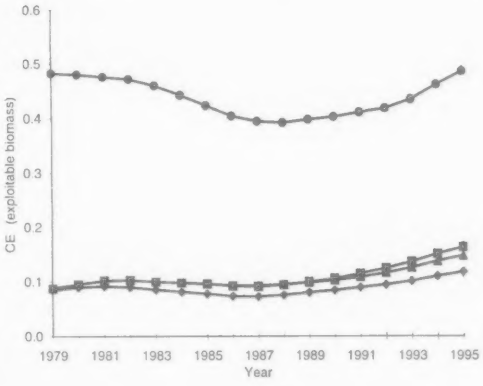


Figure 11

Coefficient of error (CE) of the exploitable biomass (thousands metric tons) versus year: asymptotic selectivity, age and length data (◆); asymptotic selectivity, age data (■); asymptotic selectivity, length data (▲); and dome-shaped selectivity, length data (●).

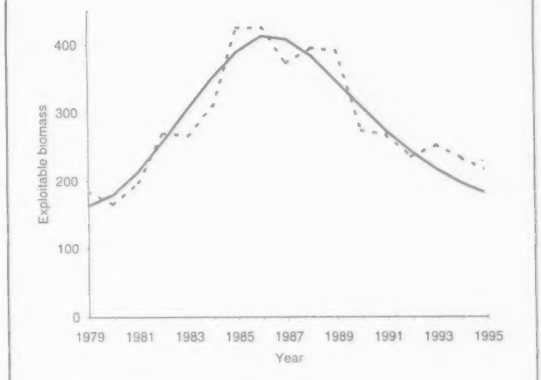


Figure 12

Estimates of exploitable biomass (thousands metric tons) by delay-difference analysis (– – –) and age-structured analysis (——).

age structure could be inferred from survey length data for the several years where no age data were available. This latter assumption may hold for sablefish, but would be conspicuously violated for other species such as Pacific halibut, *Hippoglossus stenolepis*, whose growth rate has changed over time. Recent improvements in Alaskan sablefish data collection eventually will lead to tests of these assumptions. Otoliths have been collected and read annually from longline surveys since 1995. Fishery lengths have been collected annually since 1990.

A measure of relative abundance, effort data, was necessary to obtain reasonable estimates of absolute abundance with an age-structured model of Pacific halibut, as shown by comparison to cohort analysis of historical data of year classes with complete catch data (Deriso et al., 1985). The frequency and number of the relative abundance estimates can affect abundance estimation. Absolute biomass was estimated successfully for Alaskan sablefish in this paper and for the simulated widow rockfish fishery (Bence et al., 1993). Annual surveys were simulated for 17 and 15 years, respectively. However, precise abundance estimates may not always be possible when survey effort is less. Three triennial surveys were insufficient to estimate absolute abundance for the eastern Bering Sea walleye pollock fishery with useful precision (Kimura, 1989). Species-specific simulations can help to determine the amount of survey effort necessary to estimate absolute abundance. For example, McAllister (1995) examined survey timing for assessments of the eastern Bering Sea yellowfin sole fishery. A population dynamics model was fitted to two survey time series, 1975–81 and 1982–94, then the population was projected forward 15 years and annual, versus triennial, trawl surveys were compared. Net present value of the fishery was less for more frequent surveys, primarily owing to increased survey cost, but CV (*ABC*) was less for more frequent surveys (28 versus 36%) when absolute abundance was estimated.

Parameter interactions with abundance estimates

Abundance estimates are related to estimates of several model parameters. Absolute abundance and survey catchability are inversely related because a given observation of the survey abundance index can be due to a small population that is easy to catch or to a large population that is difficult to catch. Natural mortality and catchability also are inversely related; increasing q while decreasing M tends to give similar log-likelihood values (Table 2, panel 1). Absolute abundance and natural mortality tend to be positively correlated (panel 2; Schnute and Richards, 1995). Given the observed abundance index, absolute abundance estimates must be larger for the population to sustain more natural mortality. Reducing the correlation and improving estimation of natural mortality is difficult because the number of natural deaths for marine fish species is usually unobservable; no data are available to estimate M directly. For the sablefish age-structured analysis, the overall changes in the likelihood function with respect to M were minor and not sufficient to allow estimation of M as part of the model-fitting process. I had to fix

M outside the model at the "best," most reasonable value, then estimate absolute abundance with the population model.

The likelihood surface was mapped to examine the parameter relationship between q and M (Table 2, panel 1). I found it useful to fix one parameter, then estimate the other parameter, thus ensuring that the peak of the likelihood ridge as a function of q and M was found. An alternate, seemingly useful approach is a grid over fixed values of q and M. I do not recommend this approach. It is difficult and time consuming to design a grid fine enough and large enough to map the peak of the likelihood ridge. In earlier modeling, not described in this paper, this approach led me to declare incorrectly a global minimum over q and M because the grid was too coarse and the likelihood ridge poorly mapped.

Thompson (1994) demonstrated analytically that M and the degree of curvature of dome-shape are confounded because fish may "disappear" with age, owing to natural death or decreased vulnerability. Survey catchability and selectivity also were confounded (Table 2, panel 3). Fish recruited later (panel 4) or were less vulnerable when older (panel 5), depending on the value of survey catchability. Older fish were less vulnerable when fixed q was less than estimated q (panel 5).

The lower vulnerability of older fish for lower catchability values is a clue as to why abundance estimation is less reliable when selectivity is dome-shaped. Absolute biomass is inferred in the model from how the catches affect the survey index, as described in the introduction, and this effect implies some specific estimate for absolute abundance. Older fish were less vulnerable to compensate for lower survey catchability, which helps to maintain the absolute biomass estimate implied by the catch and survey index. Estimated biomass is similar with either higher catchability or lower vulnerability of older fish, i.e. greater degree of curvature of dome-shape. This parameter interaction probably is why abundance estimation is more difficult when selectivity is dome-shaped.

In some cases, selectivity can be estimated independently to eliminate the problem of confounding parameters with selectivity. If a species is surveyed by two overlapping surveys and gear selectivity is known for one survey, then the unknown gear selectivity can be estimated by comparing the survey length compositions (Kimura, 1978). This approach helps to estimate gear selectivity, but not to estimate availability with age, where availability at age is the fraction of the population within the survey area by age. Modeling availability at age will depend on survey coverage in relation to ontogenetic changes in spatial distribution.

The age-structured model presented here is a tool for interpreting the data collected from the sablefish fishery and longline survey. Simulations and an examination of parameter relationships help one to understand how the tool performs, its reliability, and its strengths and weaknesses. The population model appears reliable for interpreting the sablefish data and has been adopted for estimating abundance and setting quotas for sablefish management. The conclusions regarding data and model requirements for estimating abundance and parameter interactions with abundance estimates should be generally applicable to other species. The sablefish age-structured model is like other north Pacific age-structured models except for the assumption of a discrete fishery. In one respect, these simulations were a more difficult test of an age-structured model to estimate abundance because one scenario examined length data alone, an imprecise measure of age structure.

Acknowledgments

The analysis benefitted from an on-going dialogue with Jeff Fujioka. I thank Dan Kimura, Jerry Pella, and Jon Heifetz for reviewing earlier versions and two anonymous reviewers for improving the presentation of this paper.

Literature cited

Alverson, D. L., and W. T. Pereyra.
1969. Demersal fish explorations in the northeastern Pacific Ocean—an evaluation of exploratory fishing methods and analytical approaches to stock size and yield forecasts. J. Fish. Res. Board Can. 26:1985–2001.

Bence, J. R., A. Gordoa, and J. E. Hightower.
1993. Influence of age-selective surveys on the reliability of stock synthesis assessments. Can. J. Fish. Aquat. Sci. 50:827–840.

Clark, W. G.
1991. Groundfish exploitation rates based on life history parameters. Can. J. Fish. Aquat. Sci. 48:734–750.

Clausen, D. M., J. T. Fujioka, and J. Heifetz.
1997. Estimates of sablefish, *Anoplopoma fimbria*, abundance in the Gulf of Alaska based on depletion experiments using longlines. *In* M. Saunders and M. Wilkens (eds.), Biology and management of sablefish, *Anoplopoma fimbria*, p. 171–182. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 130.

Deriso, R. B., P. R. Neal, and T. J. Quinn II.
1989. Further aspects of catch-age analysis with auxiliary information. *In* R. J. Beamish and G. A. McFarlane (eds.), Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, p. 127–135. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Deriso, R. B., T. J. Quinn II, and P. R. Neal.
1985. Catch-age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42:815–824.

Eggers, D. M., N. A. Rickard, D. G. Chapman, and R. R. Whitney.
1982. A methodology for estimating area fished for baited hooks and traps along a ground line. Can. J. Fish. Aquat. Sci. 39:448–453.

Engås, A., and O. R. Godø.
1989a. Escape of fish under the fishing line of a Norwegian sampling trawl and its influence on survey results. J. Cons. Int. Explor. Mer 45:269–276.
1989b. The effect of different sweep lengths on the length composition of bottom-sampling trawl catches. J. Cons. Int. Explor. Mer 45:263–268.

Fournier, D., and C. P. Archibald.
1982. A general theory for analyzing catch at age data. Can. J. Fish. Aquat. Sci. 39:1195–1207.

Fujioka, J. T.
1986. Sablefish. *In* R. L. Major (ed.), Condition of groundfish resources of the Gulf of Alaska region as assessed in 1985, p. 79–108. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-106.
1995. Sablefish. Chapter 4 *in* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska as projected for 1996, p. 1–17. [Available from North Pacific Fishery Management Council, 605 West 4th Ave., Suite 306, Anchorage, AK 99501-2252.]

Fujioka, J. T., M. F. Sigler, and S. A. Lowe.
1996. Sablefish. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska as projected for 1997, p. 189–229. [Available from North Pacific Fishery Management Council, 605 West 4th Ave., Suite 306, Anchorage, AK 99501-2252.]

Kimura, D. K.
1978. Logistic model for estimating selection ogives from catches of codends whose ogives overlap. J. Cons. Int. Explor. Mer 38:116–119.
1985. Changes to stock reduction analysis indicated by Schnute's general theory. Can. J. Fish. Aquat. Sci. 42:2059–2060.
1989. Variability, tuning, and simulation for the Doubleday-Deriso catch-at-age model. Can. J. Fish. Aquat. Sci. 46:941–949.
1990. Approaches to age-structured separable sequential population analysis. Can. J. Fish. Aquat. Sci. 47:2364–2374.

Kimura, D. K., and J. J. Lyons.
1991. Between-reader bias and variability in the age-determination process. Fish. Bull. 89:53–60.

Lowe, S. A.
1995. Sablefish. Chapter 8 *in* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions as projected for 1996, p. 1–23. [Available from North Pacific Fishery Management Council, 605 West 4th Ave., Suite 306, Anchorage, AK 99501-2252.]

McAllister, M.
1995. Using decision analysis to choose a design for surveying fisheries resources. Ph.D. diss., Univ. Washington, Seattle, WA, 293 p.

McDevitt, S. A.
1986. Sablefish. *In* R. G. Bakkala and L.-L. Low (eds.), Condition of groundfish resources of the eastern Bering Sea and Aleutian Islands region in 1985, p. 87–100. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-104.

Pope, J. G., and J. G. Shepherd.
1985. A comparison of the performance of various methods for tuning VPAs using effort data. J. Cons. Int. Explor. Mer 42:129–151.

Press, W. H., B. P. Flannery, S. A. Teukolsky, and W. T. Vetterling.
1989. Numerical recipes. Cambridge Univ. Press, New York, NY, 702 p.

Rose, C. S.
1986. A comparison of catch rates of sablefish by bottom trawls and longlines. *In* R. L. Major (ed.), Condition of groundfish resources of the Gulf of Alaska region as assessed in 1985, p. 297–304. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-106.

Schnute, J. T., and L. J. Richards.
1995. The influence of error on population estimates from catch-age models. Can. J. Fish. Aquat. Sci. 52:2063–2077.

Sigler, M. F., and J. T. Fujioka.
1988. Evaluation of variability in sablefish, *Anoplopoma fimbria*, abundance indices in the Gulf of Alaska using the bootstrap method. Fish. Bull. 86:445–452.

Thompson, G. G.
1994. Confounding of gear selectivity and the natural mortality rate in cases where the former is a nonmonotone function of age. Can. J. Fish. Aquat. Sci. 51:2654–2664.

Fisheries benefits and optimal design of marine reserves

Joshua Sladek Nowlis

Callum M. Roberts

Eastern Caribbean Center
University of the Virgin Islands
St. Thomas, Virgin Islands 00802-9990
Present address (for J. Sladek Nowlis): Center for Marine Conservation
580 Market Street, Suite 550
San Francisco, California 94104
E-mail address (for J. Sladek Nowlis): JSNowlis@cacmc.org

Abstract.—We used fishery population models to assess the potential for marine fishery reserves, areas permanently closed to fishing, to enhance long-term fishery yields. Our models included detailed life history data. They also included the key assumptions that adults did not cross reserve boundaries and that larvae mixed thoroughly across the boundary but were retained sufficiently to produce a stock-recruitment relationship for the management area. We analyzed the results of these models to determine how reserve size, fishing mortality, and life history traits, particularly population growth potential, affected the fisheries benefits from reserves. We predict that reserves will enhance catches from any overfished population that meets our assumptions, particularly heavily overfished populations with low population growth potential. We further predict that reserves can enhance catches when they make up 40% or more of fisheries management areas, significantly higher proportions than are typical of existing reserve systems. Finally, we predict that reserves in systems that meet our assumptions will reduce annual catch variation in surrounding fishing grounds. The fisheries benefits and optimal design of marine reserves in any situation depended on the life history of the species of interest as well as its rate of fishing mortality. However, the generality of our results across a range of species suggest that marine reserves are a viable fisheries management alternative.

Manuscript accepted 28 August 1998.
Fish. Bull. 97:604–616 (1999).

Fishing activity impacts the marine environment in several ways. Individual species risk severe declines from overexploitation. Over two-thirds of all fisheries world-wide are classified as fished beyond capacity or in danger of becoming so (FAO, 1995), and higher trophic levels are particularly affected (Pauly et al., 1998). Along with target species, fishing can reduce the populations of nontarget species that are caught and discarded. The ecosystems that support the fisheries also face risks. Fishing can cause biological damage to ecosystems when the reduction of key species or trophic levels causes ecological shifts (e.g. Hay, 1984; Castilla and Durán, 1985; Hay and Taylor, 1985; Durán and Castilla, 1989; McClanahan and Shafir, 1990; Roberts, 1995; McClanahan et al., 1996; Pauly et al., 1998). Fishing can also cause physical damage to ecosystems, particularly when dwindling fish catches promote the incentive to use damaging fishing practices (McAllister, 1988).

Reserves can protect the ecosystems within them from damaging fishing practices and have the potential to reestablish a natural ecosystem balance (Russ, 1985; Plan Development Team, 1990; Roberts and Polunin, 1991; Dugan and Davis, 1993; Roberts and Polunin, 1993; Rowley, 1994; Roberts et al., 1995; Bohnsack, 1996). Field studies have generally demonstrated that fish stocks build up within a protected area (Roberts and Polunin, 1991; Dugan and Davis, 1993; Rowley, 1994; Bohnsack, 1996, and references within) but much less information exists on fishery enhancements.

In theory, reserves can maintain productive fisheries by protecting a critical stock within their borders. These stocks may enhance catches through adults that grow larger in the reserve and then migrate to fishing areas (adult spillover), or through enhanced recruitment in fishing areas due to increased population fecundity from the reserve (larval transport). In practice, fisheries benefits from reserves have rarely been demonstrated or even measured. This lack of field evidence reflects the difficulty of performing controlled and replicated experiments in unpredictable political and biological systems.

The few existing field studies addressing fisheries benefits from reserves show promise. A marine fishery reserve encompassing over 60% of the former fishing grounds north of Mombasa, Kenya, showed a 110% increase in catch per unit of effort after only two years (McClanahan and Kaunda-Arara, 1996). Total catches had not yet met those prior to reserve establishment, but trends looked favorable. On Apo Island, Philippines, total fish density and

species richness had increased by over 400% in both the reserve and the fishing grounds after 11 years of reserve protection (Russ and Alcala, 1996). Large fish were particularly abundant in the fishing grounds near the border of the reserve, possible evidence of adult spillover. These same authors showed previously that overall catches dropped more than 50% two years after the re-opening of a closed area on Sumilon Island, Philippines, despite the increased fishing area (Alcala and Russ, 1990), suggesting that the reserve had provided enhancements to surrounding fishing grounds.

These field studies show that under certain circumstances, reserves are likely to produce fisheries enhancements. However, models are also necessary because they allow more general analyses of the conditions under which reserves are likely to produce benefits and of the design attributes that will maximize these benefits. By making use of controlled replicates and large-scale manipulations, models can provide a theoretical background on which to interpret field results.

Several authors have built and analyzed models of marine fishery reserves. These models can be classified as those examining adult spillover (Beverton and Holt, 1957; Polacheck, 1990; DeMartini, 1993) and those examining larval transport (Quinn et al., 1993; Man et al., 1995; Holland and Brazee, 1996; Sladek Nowlis and Roberts, 1997; Holland et al.[1]). All of these models predict fisheries enhancements from reserves in at least some situations, particularly under heavy exploitation. However, the predicted enhancements were small and uncommon for the adult spillover models. Previous models have examined a variety of factors that influence potential reserve benefits, including adult movement tendencies (Polacheck, 1990; DeMartini, 1993), individual growth rate (DeMartini, 1993), Allee effects (Quinn et al., 1993), metapopulation patch dynamics (Man et al., 1995), and socioeconomic factors (Holland and Brazee, 1996; Holland et al.[1]). None of these examined the effect of population growth potential on reserve benefits.

In order to fill this gap, we built a set of models looking at reproductive enhancement and larval transport as mechanisms for providing reserve benefits. We analyzed these models with particular emphasis on how reserve size, fishing mortality, and life history traits, particularly population growth potential, affect long-term fishery yields. We also analyzed the short-term consequences of reserve establishment and these results are presented elsewhere (Sladek Nowlis and Roberts, 1997).

We used our models to achieve several goals. First, we wanted to identify conditions that favored the success of reserves at enhancing fisheries. Second, we wanted to establish design criteria to help maximize the benefits that could accrue from a closed fishing area. Third, we wanted to assess whether reserves can decrease year-to-year variation in catches. Finally, we wanted to provide guidelines for future field research through the identification of important but poorly understood biological processes and through the generation of testable predictions about the design and function of marine fishery reserves.

Methods

Our basic model followed yearly changes in a population separated into size categories. Although categorization by age is more common than by size, we felt size better represented size-dependent processes such as reproduction and fishing mortality (Polunin and Roberts, 1996). Each size category contributed to future populations through some simple rules (Fig. 1).

We used the best-available estimates of size-based fecundity and larval survivorship for various species (see Table 1). Little is known about larval survivorship in fish, especially for coral reef species (Boehlert, 1996). The best estimates we could find came from an analysis of larval performance across a global array of ambient temperatures (Houde, 1989). Houde used linear regression on data from various studies to relate ambient temperature to fish larval duration and daily survivorship. This process produced statistically significant and predictive, but crude, relationships that could then be combined to estimate total larval survivorship. At a temperature of 26°C, Houde's estimate of survivorship for larvae through the entire larval stage was 5×10^{-5} (see Appendix for equations). Whenever we had additional information about larval stage duration, we used it along with Houde's temperature-based estimate for daily survivorship to produce our estimate of total larval survivorship.

Natural mortality estimates were also taken from the literature (see Table 1). Those adults that survived had the additional possibilities of either growing to the next size class or staying in the same one. We used von Bertalanffy growth parameters (Ricker, 1975) to determine the chance that a fish of one size class grew to the next in a given year (Fig. 2). Von Bertalanffy parameters describe the growth of individual fish and are widely estimated in the literature (see Table 1 for the estimates that we used and

[1] Holland, D. S., J. B. Braden, and R. J. Brazee. 1995. Managing artisanal fisheries with marine fishery reserves: an alternative to managing catch or effort. Environmental and Natural Resources Policy and Training/Midwest Universities Consortium for International Activities Supplementary Paper 3, 36 p.

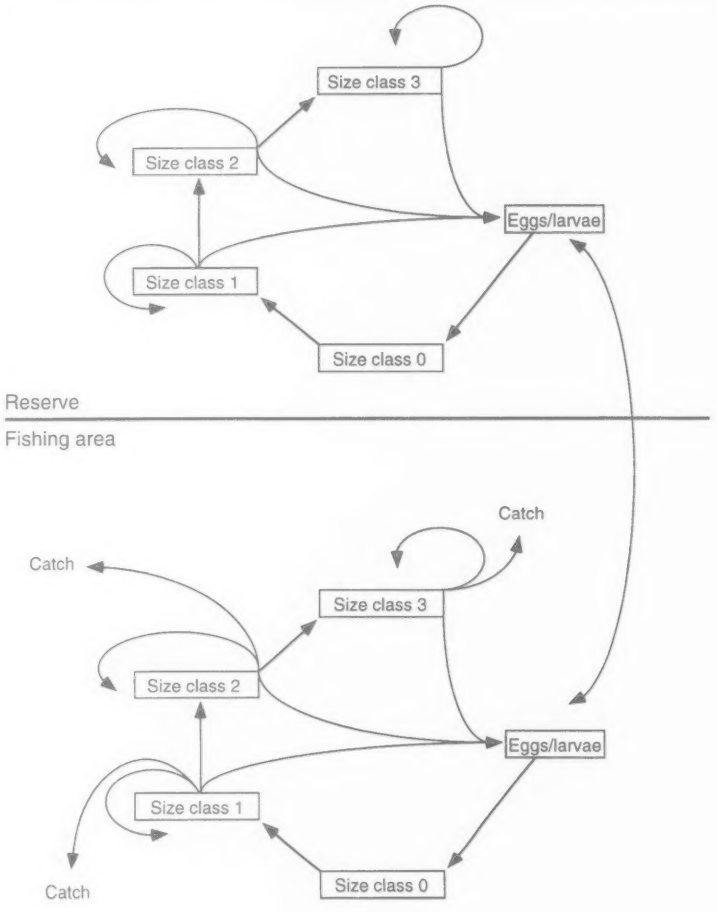


Figure 1

Flow diagram for the model. Lines represent contributions from one size class to itself and others. Populations in the fishing area and reserve interacted through larval dispersal between them, whereas adults remained in the area where they settled. Populations in the fishing area experienced fishing mortality ("catch"), whereas reserve populations did not. Otherwise, populations in reserve and fishing areas experienced the same population phenomena. This figure is an example of the model construction for white grunt, *Haemulon plumieri*—the number of size classes, size class at reproductive maturity, and size class at recruitment to the fishery differed for other species.

Appendix for relevant equations). To convert these continuous measures into probabilities, we used the standard von Bertalanffy parameters to estimate the lengths of the smallest and largest individual in each size category for the following year. We calculated the proportion of this size range that fell into the next size class and used this value to represent the probability that a fish of this size class grew to the next size class. The remaining individuals stayed the same size over the next year, with a probability determined by subtracting the probability of growing from 1. We chose the size-class interval for each species such that newly settled fish had exactly 100% chance of growing to the next size class during the first year (see Appendix for formula). Consequently, fish were never able to grow more than one size class in a year. As with all von Bertalanffy growth relationships, growth slowed with age—in our case from

Table 1

Parameter values for four fishery species. See Appendix for detailed explanation of parameters. Parameter values were taken from the literature where available. Where we could not find values in the literature, we made our best educated guess by looking at a related species, by running several values until we got realistic population growth (i.e. growth in the absence of fishing), or by measuring some other consequence, for example length at recruitment, to check for realism. References: (1) Plaut (1993); (2) Houde (1989); (3) Plaut and Fishelson (1991); (4) Aiken (1983); (5) Darcy (1983); (6) Thompson and Munro (1983); (7) best guess.

Species	Fecundity	Larval survival	Adult survival	Growth
Panulirus penicillatus, Red Sea spiny lobster	r = 4 spawns per year × 2.715 × $L^{2.581}$ eggs per spawn Mature at L = 50 mm (1)	D = 35.5 days (1) Z = 0.3454 (2) $N = 5 \times 10^{-6}$ (2)	v = 0.8 (M=0.223) Fishery recruitment = 25.7 mm (7)	k = 0.1066 L_∞ = 84.7 mm t_0 = 0 c = 6.43×10^{-4} y = 2.89 (3)
Balistes vetula, queen triggerfish	r = 3 spawns per year × 73 per g body weight Mature at size 23.5 cm (4)	D = 28.7 days (2) Z = 0.3454 (2) $N = 5 \times 10^{-5}$ (2)	v = 0.07427 (M=2.6) (4) Fishery recruitment = 17 cm (7)	k = 0.57 (4) L_∞ = 45 cm (4) t_0 = –0.5 (7) c = 0.05164 (4) y = 2.875 (4)
Haemulon plumieri, white grunt	r = 1 spawn per year × (626 per g body weight – 93000) Mature at size = 22 cm (5)	D = 28.7 days (2) Z = 0.3454 (2) $N = 5 \times 10^{-5}$ (2)	v = 0.17 (M=1.77) Fishery recruitment = 14.9 (5)	k = 0.34 (5) L_∞ = 42 (5) t_0 = –1 (7) c = 0.0238 (5) y = 2.93 (5)
Epinephelus guttatus the red hind	r = 1 spawn per year × 873.454 per g body weight – 194086) Mature at size < 25 cm (6)	D = 28.7 days (2) Z = 0.3454 (2) $N = 5 \times 10^{-5}$ (2)	v = 0.5066 (M=0.68) Fishery recruitment = 31 cm (6)	k = 0.24 (6) L_∞ = 52 (6) t_0 = –0.5 (7) c = 0.0107 (6) y = 2.96 (6)

100% growth for new settlers to 0% for fish in the largest size class.

Adults in the fishing area that grew larger than the minimum catch size experienced fishing mortality. We represented fishing mortality using the parameter u, equal to the proportion of fishery-recruited individuals caught per year, and related to the more common F by the equation:

$$u = 1 - e^{-F}.$$

We independently varied the two key parameters in our models: fishing mortality (u) and reserve proportion (s).

We made settlement a density-dependent process by incorporating a negative exponential function into survivorship for new settlers during their first year (see Appendix for equation). There is evidence to suggest that shelter is limiting for coral reef fish, especially new settlers (Hixon, 1991; Hixon and Beets, 1993; Hixon and Carr, 1997)—a process that would fit well with our density dependence assumptions. We also performed runs in which larval rather than new settler survivorship was density-dependent and

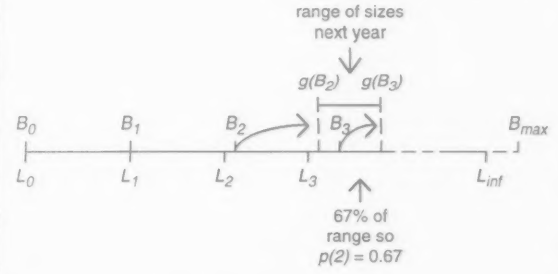


Figure 2

Determination of growth probabilities. The probability $p(x)$ that a fish of size class x grows to size class x+1 is the proportion of the range of sizes that size class x individuals will span one year later. Using von Bertalanffy growth parameters (see Appendix), we determined one year in the future the size of the smallest and largest fish in size class x. All other fish in x would fall between these two values. We then determined what proportion of these sizes fell into size class x+1, 0.67 in the case illustrated. In this hypothetical example, we would assume that $p(x)$ = 0.67, or that 67% of the fish from size class x grew to class x+1 by the next year. L_t represents the sizes attained at age t and B_x represents the lower bounds of each size class. We begin counting age at the moment of settlement (so $L_0 = B_0$).

obtained qualitatively identical results. Little information exists on density-dependent relationships for tropical fish; therefore we were forced to use a standard theoretical logistic equation (see Appendix). For simplicity in analysis and in recognition of this knowledge gap, we constructed the models with a fixed carrying capacity of 1000 one-year-old individuals per unit area. We modeled population processes on the basis of density measures in reserve and fishing areas and used relative proportions of each to calculate catches and population fecundity. Thus, yields are expressed as kg per year from the whole management area.

In order to ask the general questions we intended, we used two simple movement assumptions that emphasized the benefits accruing from larval transport rather than from adult spillover. Larvae dispersed widely across reserve boundaries, resulting in an even density of new fish settlement in reserve and nonreserve areas. This assumption does not negate the possibility that larvae drift to the open ocean and become lost—these can be accounted for in larval mortality. Rather, the assumption implies that settlement in the reserve and the management area are equally affected by the stock averaged over both areas. We also assumed that adults did not move across reserve boundaries; that is to say fish spent their entire lifetime in the area in which they settled. These assumptions specifically addressed the case where enhanced fecundity within the reserve was exported to fishing areas through larval transport. Thus they complemented previous models that focused on enhancements from adult spillover (Polacheck, 1990; DeMartini, 1993). These models also examined potential increases in reproductive output by means of increased spawning stock biomass per recruit. However, they were unable to examine the equilibrium consequences with their particular model construction.

Our movement assumptions apply to the majority of fishery species on at least some spatial scales. Most aquatic species disperse more widely as larvae than as adults (Boehlert, 1996). Consequently, larvae are more likely to cross boundaries than are adults. As long as individual reserve units stretch beyond the dispersal distance of adults but remain well within the dispersal distance of larvae for a given species, the model assumptions will approximate reality. For large reserve proportions, our assumptions could still be met if the reserve area were partitioned into several smaller units. Some areas of concern here include ontogenetic and reproductive migrations. To fit the assumptions of this model, reserves must be designed with these movements in mind so that fish are likely to remain in the reserve during the phase of their life in which they are vulnerable to fishing.

We ran the models over reserve proportions varying from 0 to 99% of the management area (s=0 to 0.99), and fishing mortalities varying from 1% to 100% mortality of fishery-recruited individuals per year (u=0.01 to 1.00). For each combination of fishing mortality and reserve proportion, the model ran until the fish catch—calculated for the whole management area rather than per km^2 of available fishing area—had stabilized at the long-term sustainable yield. The model stored the yield, fishing mortality, and reserve proportion. It sometimes took hundreds of years to reach stability, and those interested in our model's predictions about the short-term dynamics of reserve creation should refer to Sladek Nowlis and Roberts (1997).

We used these results to determine the optimal reserve proportions and fishing mortalities for individual fishery species. For each fishing mortality, we found the reserve proportion that maximized sustainable yields and stored it and the yield. We compared these yields when an optimally-sized reserve was used with the yields without a reserve (s=0) to establish fisheries benefits. We plotted this information using fishing mortality as an independent variate.

We also examined the effects of marine fishery reserves on year-to-year catch variability. Bohnsack (1996) suggested that marine fishery reserves could dampen natural fluctuations in catches, thus making fisheries more stable and easier to manage. We tested this hypothesis by adding a stochastic component to larval survivorship in our model. These new models drew larval survivorship randomly from a normal distribution around the mean larval survivorship whose standard deviation we could define. We examined all species over a range of fishing mortalities and present the results from u = 0.2, 0.4, 0.6, and 0.8 to illustrate the pattern. We also examined some of these conditions at three levels of environmental variation, with standard deviations of 5, 10, and 20% of the mean larval survivorship, to gain insight into whether reserve benefits are influenced by the degree of environmental variability.

For each possible combination of fishing mortality and reserve proportion, we performed 10 replicate runs of our stochastic models. In each run, we ran the models for 500 years to allow the fisheries to stabilize to the maximum extent possible and thus minimize the influence of our arbitrarily chosen initial state. The mean and standard deviation of the catches were measured over the next 100 years. We examined the ratio of the standard deviation to the average catch over this period because this measure gave us an estimate of the likelihood of percentage fluctuations in catches rather than absolute changes.

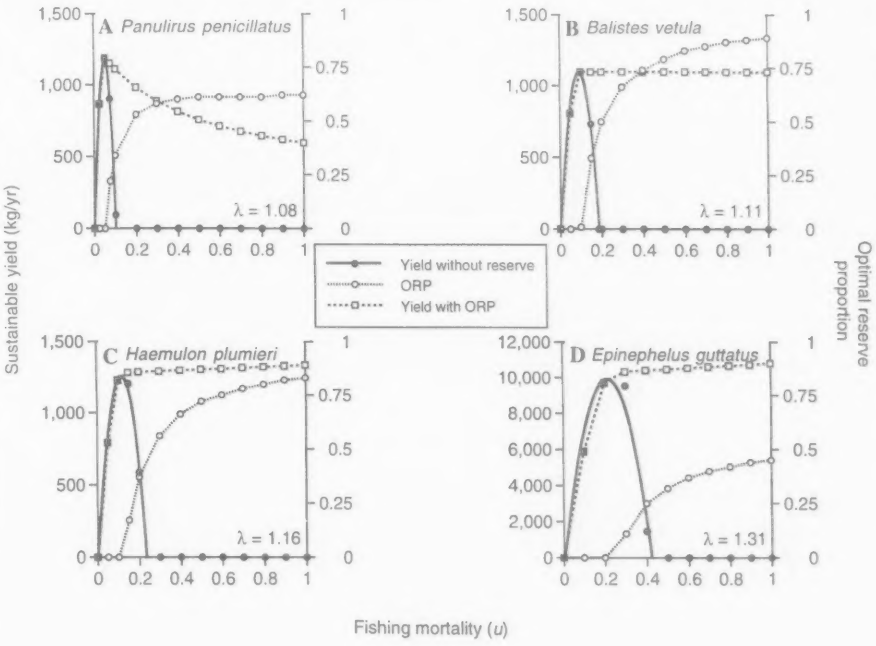


Figure 3

Optimal reserve proportions and corresponding yields. (**A**) *Panulirus penicillatus*, Red Sea spiny lobster. (**B**) *Balistes vetula*, queen triggerfish. (**C**) *Haemulon plumieri*, white grunt. (**D**) *Epinephelus guttatus*, red hind. In all graphs, the solid circles and line represent the sustainable yield (kg of catch per year from the whole management area) that occurs in the absence of a reserve, the open circles and dotted line represent the optimal reserve proportion (that which produced maximum sustainable yields for each fishing mortality), and the dashed line and squares represent the sustainable yield when the optimal reserve proportion was used. Intrinsic population growth rates (λ) determine the robustness of the populations to fishing, high growth rates sustaining heavy fishing and low rates requiring reserves at low fishing mortalities.

This measure is better than standard deviation alone which would treat a 10-kg fluctuation equally, regardless of whether it occurred in a 100 kg or 1,000,000 kg per year fishery. We graphed these results with reserve proportion as the independent variate and examined the graphs for trends.

We performed these analyses on four coral reef fishery species for which we obtained relatively complete parameter sets. These included *Balistes vetula*, queen triggerfish; *Epinephelus guttatus*, red hind; *Haemulon plumieri*, white grunt; and *Panulirus penicillatus*, Red Sea spiny lobster (see Table 1 for parameter estimates).

Results

When we ran the models without a reserve (s=0), they produced standard yield-effort curves (Fig. 3). These curves are characterized by steep initial gains in long-term sustainable yields with increases in fishing mortality (and thus effort), followed by equally steep declines (Clark, 1990). The curves peaked at the maximum sustainable yield, one of several goals a manager might try to achieve with a fishery (Clark, 1990), and we will refer to the corresponding fishing mortality as the MSY mortality for the rest of this paper. Above the MSY mortality, the fishery can be defined as overfished because it is less productive than it would be with less fishing activity.

When a reserve was present, the yield-mortality curves were still parabolas passing through the origin but spread farther to the right, and the larger the reserve, the more pronounced were these shifts. Consequently, larger reserves required higher fishing mortalities to maximize long-term sustainable yields (remember that this mortality only affected fish in fishing areas), whereas the sustainable yields

decreased more slowly as fishing mortality increased past the MSY mortality.

Our analyses of optimal reserve proportions produced several key results. First, reserves produced fisheries enhancements, meaning that the overall catches with a reserve exceeded those without one, whenever the fisheries were overfished (Fig. 3), here defined as fished above the MSY mortality level. When fisheries were overfished, they produced higher yields with a reserve even though the reserve decreased the amount of fishing area. The optimal reserve proportion increased with increasing fishing mortality, and heavily exploited fisheries required particularly large reserves to remain productive. The fishery benefit attributable to reserves, calculated by subtracting the yield without a reserve from that with an optimally sized reserve, increased with increasing fishing mortality up to a near-maximum yield in most cases (Fig. 4). Consequently, a wide span of reserve sizes (up to 80% of the management area for some species) produced similarly high yields for most species as long as fishing mortalities were chosen accordingly.

Using this information (Fig. 3), we predicted optimal reserve proportions under real-life fishing mortalities. For queen triggerfish, the fishing mortality estimate of $u = 0.45$ from Puerto Rico and the Virgin Islands (Aiken, 1983) corresponded to an optimal reserve proportion of approximately $s = 0.8$. For white grunt, a reported heavy fishing mortality of $u = 0.99$ from Jamaica (Darcy, 1983) corresponded to an optimal reserve proportion of just over $s = 0.75$. Thus, for these species in these locations, our models predicted that 75–80% of the fishing grounds should be made off-limits to fishing in order to maximize long-term sustainable yields. These numbers may seem unrealistically high, especially since most models predict maximum yields when approximately 50% of the population density at carrying capacity is protected from fishing (see Clark, 1990, for an overview). In the case of our models, populations within the reserve did not reach carrying capacity when fishing was heavy outside, and the conditions of peak production corresponded to those that protected approximately 50% of the population density at carrying capacity.

The qualitative conclusions outlined above were consistent across all the species we examined. However, the model's quantitative predictions of the long-term fishery yields and optimal reserve proportion varied from species to species for any given fishing mortality (Fig. 3). The key differences between species were the speeds at which the yield and optimal reserve proportion changed with increasing fishing mortality (Fig. 3). These differences reflected differences in intrinsic population growth rates (λ)—the maximum growth rate of a population with no density-dependent constraints or fishing mortality. This summary parameter integrates most of the life history data that we used. It does not include the growth rate of individuals in the population and consequently does not adequately predict yields. However, it is a useful summary of the ability of a population to sustain harvesting. For example, life history parameters from the literature suggested that the Red Sea spiny lobster had a relatively low $\lambda = 1.08$, just above the $\lambda = 1$ necessary for a population to sustain itself with no fishing pressure. This species had a low MSY fishing mortality because its slow population growth could

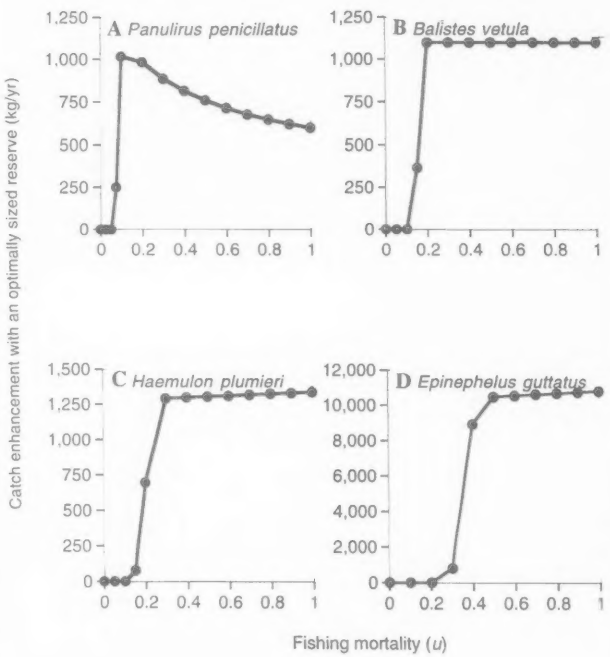


Figure 4

Catch enhancements with the use of an optimally proportioned reserve (OPR). (**A**) *Panulirus penicillatus*, Red Sea spiny lobster. (**B**) *Balistes vetula*, queen triggerfish. (**C**) *Haemulon plumieri*, white grunt. (**D**) *Epinephelus guttatus*, red hind. Values represent the increase in yield, in kg of catch per year from the whole management area, one could expect if an optimally sized reserve system were established in a management area that lacked reserves initially.

only sustain modest harvesting effort (Fig. 3). In contrast, life history parameters from the literature suggested that red hind had a relatively high $\lambda = 1.31$. Consequently, its maximum sustainable yield occurred at the highest fishing mortality of any species we tested (Fig. 3). The two other species we examined had intermediate intrinsic rates of population growth rates and responses to reserves.

The sensitivity of our models' quantitative predictions was also clear within a species when we varied larval survivorship. For all species, optimal reserve proportion and yield without a reserve varied greatly (senior author's unpubl. data) because we varied larval survivorship from 10^{-5} to 10^{-4}. This sensitivity to poorly understood parameter values renders any quantitative estimates of optimal reserve proportion unreliable, whether the inaccuracy is in larval survivorship, the relationship, or parameters for density dependence, or any other life history parameter.

Finally, we examined how reserves might influence unpredictable catches resulting from environmental variation. Our stochastic models predicted that catches will be more stable with larger reserve proportions. In these models, we saw general decreases in catch variability with increasing reserve proportion (Fig. 5). The results presented here showed drops in variation that were more pronounced at higher fishing mortalities for all four species. We also tested these results at three levels of environmental variation. Our results showed that the drop in catch variability was most extreme when the environment was most variable, suggesting that the stability offered by reserves will be most valuable in highly variable fisheries.

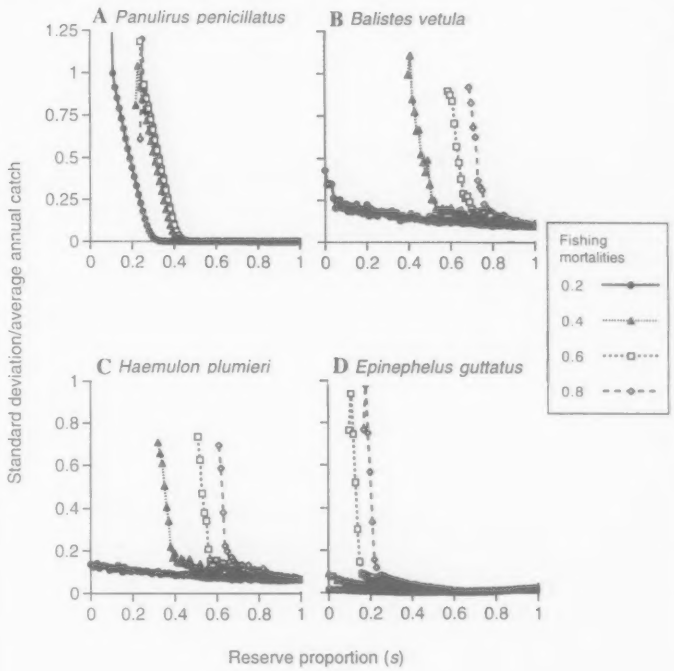


Figure 5

Catch variability and reserve size. (**A**) *Panulirus penicillatus*, Red Sea spiny lobster. (**B**) *Balistes vetula*, the queen triggerfish. (**C**) *Haemulon plumieri*, white grunt. (**D**) *Epinephelus guttatus*, red hind. Each graph shows decreasing catch variability with increasing reserve proportion at four levels of fishing mortality.

Discussion

Effects of life history and fishing mortality on reserve benefits

Our models predicted that marine fishery reserves will provide catch enhancements to any overfished fishery that meets our basic assumptions regarding the movement of adults and larvae. The results from previous modeling efforts by Man and colleagues (1995) and Holland and co-workers (Holland and Brazee, 1996; Holland et al.[1]) support these findings if one compares their results in specific cases to the patterns we found for a variety of species. Two key variables help determine whether a population is overfished: intrinsic population growth rate (λ) and fishing mortality. Managers can control fishing mortality to varying extents. Apparently, this control is inadequate in many industrial fisheries (FAO, 1995) and is probably even less effective in subsistence fisheries (Roberts and Polunin, 1993). Managers have no control over population growth potential but can take into account that species with low population growth have a greater tendency to be overfished and consequently show greater promise for fisheries enhancements from reserves.

Even in a well-managed fishery, it may be helpful to close large areas. This strategy could allow the relaxation of some fishing restrictions in remaining waters. Consequently, recreational and commercial

fishermen may feel greater equity with fewer restrictions on the number of participants or their catches. Moreover, reserves have the potential to reduce variability in catches from year to year and to enhance conservation of species and ecosystems. Fishing is not the only threat to marine ecosystems, though, and fisheries regulations are not sufficient to protect these systems (Allison et al., 1998).

To our knowledge, no field study has yet examined the effects of population growth potential or fishing mortality on reserve benefits. In part, such studies are made difficult by the uncontrolled nature in which reserves are established.

Relation of fishery benefits to reserve size

Real-world fisheries span a range from lightly fished to heavily overfished, and the optimal reserve size will depend on the fishing mortality as well as the population growth potential of the target species. Because many fisheries involve multiple species with widely divergent population growth potentials, choosing a single best reserve size may be difficult. Moreover, key aspects of the life history of marine fish, the larval phase in particular, remain a mystery. Because of these gaps in knowledge, it would be difficult to make an accurate prediction of the optimal reserve size even in a well-studied single-species fishery.

Although our research sheds doubt on the use of a universal reserve proportion, it does lend support for the use of large reserve systems under certain circumstances. In the two real-world cases where the necessary information existed, our models predicted that reserves should encompass 75–80% of the management area. These proportions are enormous and may be unrealistic for several reasons. First, the short-term economic losses from closing 80% of a management area would be large, although our models predict that the recovery time for such heavily overfished fisheries would be rapid (Sladek Nowlis and Roberts, 1997). Second, the political challenges of establishing such large reserves would be a formidable barrier. Finally, we do not stand firmly behind these predictions because their accuracy is dependent on parameter values that are poorly understood. Nevertheless, consistent results across several species suggest that reserves encompassing 40% or more of a heavily fished management area could produce substantial fisheries benefits.

Though rare, at least one large reserve system does exist. The Mombasa Marine National Park closed over 60% of local fishing grounds (McClanahan and Kaunda-Arara, 1996). This example fits nicely with our model's assumptions because levels of fishing effort remained similar in the fishing grounds before and after the closure. After two years, total yields had not surpassed those prior to reserve establishment (McClanahan and Kaunda-Arara, 1996). However, catch per unit of effort had increased dramatically and total yields showed potential for future increases. In this case and others involving extensive use of marine reserves, our research encourages an adaptive approach that reflects the lack of knowledge about fish life histories and the high degree of uncertainty in these complex biological systems.

Relation of reserve size to catch variability

Our model supported Bohnsack's (1996) hypothesis that catch variability will decrease with increasing reserve size. Our models predicted decreases in catch variability across a variety of levels of environmental variability and fishing mortalities. Our results also complement other studies that showed that reserves could reduce catch variability,[2] decrease the likelihood of bad years (Lauck et al., 1998), and increase the persistence of fisheries vulnerable to overfishing (senior author's unpubl. data).

To our knowledge, no field study has yet examined the effects of reserves on catch variability. Although they may be confounded by variability in fishing effort, the necessary data should be practical to collect before and after reserve creation.

Assumptions revisited

As with all models, one must be careful in interpreting the results of this one. It is based on parameter values that in some incidences—larval survivorship in particular—are poorly understood. However, the model's predictions are qualitatively robust to parameter errors, meaning that its general predictions hold true across a wide range of values and a wide variety of species. Our assumptions regarding the movement of adults and larvae were far more critical in influencing the conclusions we have drawn here.

Our assumptions regarding adult movement have wide applicability. Many fisheries target sessile organisms such as harvested kelp (Bustamente and Castilla, 1990), slow-moving organisms including many invertebrates (Davis and Dodrill, 1980; Davis and Dodrill, 1989), and organisms with high site-specificity such as many reef fish (Polunin and Roberts, 1996). All of these systems are likely to approximate our assumptions of no adult movement. This model is not universally applicable, as highly mobile and migratory species, including many pelagic fisher-

[2] Mangel, M 1998. Environmental Studies Board, University of California, Santa Cruz, CA 95064. Unpubl. data.

ies (Safina, 1993), will only fit our adult movement assumptions if large reserves are established. Recent studies, though, have shown high site fidelity by fish species previously thought to range widely (Holland et al., 1993; Holland et al., 1996), demonstrating the need for more field data on adult movement patterns. Moreover, recent modeling efforts by Holland and colleagues[1] and others[3] suggest that reserves can benefit highly mobile species through enhanced population fecundity gained from temporary protection.

If adults do cross reserve boundaries, our predictions regarding fisheries benefits from reserves will be influenced in opposing ways. Under heavy fishing pressure and intermediate movement tendencies, minor yield enhancements may be possible from this adult spillover (Polacheck, 1990; DeMartini, 1993). However, this same movement would dilute the ability of reserves to enhance larval transport to fishing areas. As Polacheck showed (1990), spawning stock biomass, or the potential for fisheries enhancement through larval transport, is highest at lowest levels of adult movement. Because the potential benefits from larval transport presented here far outweigh those predicted from adult spillover (Polacheck, 1990; DeMartini, 1993), it is likely that adult movement across boundaries will decrease the predicted yields from reserves. Consequently, reserves will have the highest potential for enhancing surrounding fisheries if they are designed as a collection of units large enough to contain populations of adults with relatively little movement across boundaries.

Our assumptions regarding larval transport have less supporting evidence. Most aquatic species disperse more widely as larvae than as adults (Boehlert, 1996), and the potential for long-distance dispersal across reserve boundaries is great for species with long-lived larvae (Roberts, 1997), including most food fish. Consequently, larvae are likely to move from reserves to fishing areas as long as oceanographic conditions and larval behavior permit. Without larval transport, the potential for fisheries benefits from reserves is more limited, although Holland and colleagues[1] did show that a reserve system in which larvae stayed in place but adults moved widely across boundaries could produce some benefits. Reserves, especially in heavily overfished or large management areas, may need to be partitioned into several subunits that maintain adult populations within them but allow larvae to disperse to remaining fishing areas.

We also assumed a stock-recruitment relationship, implying that a significant portion of the population fecundity from reserves stays in or returns to the management area. The degree to which marine populations are locally sustained remains an active area of debate in marine ecology. Larvae of most tropical food fish are often found in greatest quantities offshore (Boehlert, 1996), suggesting the possibility of long-distance dispersal. However, studies that show this result may be biased because sampling within the complex structure of the reef itself is difficult (Boehlert, 1996). Therefore, reefs may harbor greater concentrations of larvae than are measured above the reef. This complexity (Wolanski and Sarsenski, 1997), along with potential for larval behavior to influence their distribution (e.g. Breitburg et al., 1995), suggests that larvae may be retained at higher concentrations than predicted by simple oceanographic models (e.g. Roberts, 1997). If recruitment dynamics are influenced on a much larger spatial scale than encompassed by the management area, such that the stock in the management area has a minimal impact on recruitment back to it, reserve benefits to the management area are likely to be much more limited. Cohort models, including those by Polacheck (1990) and DeMartini (1993), can be interpreted as situations in which larval supply is constant and not influenced by local stock. As has been discussed, these models show limited potential for fisheries benefits from reserves. It is necessary to think of reserve systems at a scale that fits stock-recruitment relationships. Yet our knowledge of these relationships remains poor. Even if larvae have the potential to disperse over large distances, stock-recruitment relationships could still exist on a local level if a significant portion of larval production is retained. The safest approach to this uncertainty is to design reserve systems at large scales. However, there is still the potential for reserves to produce fisheries benefits on small scales if larvae have the capacity to be retained. Further research on stock-recruitment relationships in marine populations will be invaluable for resolving this pressing issue along with many others in fisheries management.

Field needs and testable predictions

Our results identify areas in need of additional field work and make testable predictions. The needs in regard to field work differ for our quantitative and qualitative predictions. The quantitative predictions were highly sensitive to all parameters that affected intrinsic population growth potential. The most important and least understood of these parameters is larval survivorship. We need significantly better information about the duration of the egg and larval stages of coral reef fishes and their daily mortality

[3] Guenette, S. 1998. Fisheries Centre, University of British Columbia, 2204 Main Mall, Vancouver, BC V6T 1Z4, Canada. Unpublished data.

risk. Until we understand these life history stages better, it will be impossible to make quantitatively accurate predictions of the optimal design of any fishery management strategy.

We also need better insight into how fecundity changes with size. Fecundity-size relationships should be fairly easy to measure and can be incorporated into any standard fishery study where adequate numbers of adults are sampled. We would further benefit from estimates of size-specific natural mortality. Few natural mortality estimates for coral reef fish species exist in the literature, and most that do are based on highly indirect methods of association. Marine fishery reserves actually offer the potential to generate more accurate predictions of natural mortality because fishing mortality does not confound the attempt in unfished areas. Moreover, despite numerous studies, we still have a poor understanding of population regulation and density dependence in coral reef fishes. This understanding is also necessary before we can generate accurate quantitative predictions of reserve benefits.

In contrast to the long list necessary to generate quantitative predictions, our qualitative predictions require additional knowledge in only one key area: fish movement. Because the qualitative predictions were robust across life history patterns, the key to knowing whether a fish species fits our assumptions is the movement of this species as eggs, larvae, and as adults. To some extent, we can skirt this issue because in our model, reserve size was based on proportion of coastline rather than actual size. Consequently, if we choose the management area to match the scale of fish movement, our model can fit most species. For example, a 20% reserve divided into areas of tens of hectares might ensure that adults of the species we examined here will stay in the area in which they settled while their larvae disperse widely among the reserve and nonreserve areas. In contrast, the management area might have to encompass whole ocean basins for the movement assumptions to fit bluefin tuna (Safina, 1993). Thus, we need to understand the movement dynamics of larvae and adults of a species to know the scales at which it will fit the assumptions of our model.

From the species that we ran and the resulting qualitative predictions of our model, we can generate a list of testable predictions. We predict that

1) Reserves will be beneficial for any over-fished population. Populations with low intrinsic growth rates and high fishing mortality stand to benefit the most, as is the case for the majority of reef fisheries in many regions of the world, such as the Caribbean. The location and size of the reserve will also affect reserve benefits. For a fair test of this prediction, reserve should be representative of typical fish habitat and large enough to contain a viable population of adults.
2) Although no universal best reserve proportion exists, we predict reserves will enhance fishery productivity even when they encompass areas much larger than those of current reserve systems.
3) Reserves will reduce variation in catches resulting from unpredictability in fishing mortality as well as recruitment strength and larval survivorship. Such an effect will simplify fishery management and increase the ability of fishermen to predict future income.

Acknowledgments

We gratefully thank the U. S. Agency for International Development and its Research Program for Historically Black Colleges and Universities as well as the University of Puerto Rico Sea Grant College Program and the National Research Council's Research Associate Program for generous support of the research reported here. We also extend our gratitude to Hilconida Calumpong of the Silliman University Marine Laboratory, who provided inspiration for this work, and to Rebecca Sladek Nowlis, who provided valuable suggestions on drafts of the manuscript.

Literature cited

Aiken, K. A.
1983. The biology, ecology and bionomics of the triggerfishes, Balistidae. *In* J. L. Munro (ed.), Caribbean coral reef fishery resources, p. 191–276. International Council for Living Aquatic Resources Management, Manila.

Alcala, A. C., and G. R. Russ.
1990. A direct test of the effects of protective management on abundance and yield of tropical marine resources. J. Cons. Int. Explor. Mer 47:40–47.

Allison, G. W., J. Lubchenco, and M. H. Carr.
1998. Marine reserves are necessary but not sufficient for marine conservation. Ecol. Appl. 8:S79–92.

Beverton, R. J. H., and S. J. Holt.
1957. On the dynamics of exploited fish populations. Chapman and Hall, New York, NY, 533 p.

Boehlert, G. W.
1996. Larval dispersal and survival in tropical reef fishes. *In* N. V. C. Polunin and C. M. Roberts (eds.), Reef fisheries, p. 61–84. Chapman and Hall, London.

Bohnsack, J. A.
1996. Maintenance and recovery of fishery productivity. *In* N. V. C. Polunin and C. M. Roberts (eds.), Reef fisheries, p. 283–313. Chapman and Hall, London.

Breitburg, D. L., M. A. Palmer, and T. Loher.
1995. Larval distributions and the spatial patterns of settlement of an oyster reef fish: responses to flow and structure. Mar. Ecol. Prog. Ser. 125:45–60.

Bustamente, R. H., and J. C. Castilla.
1990. Impact of human exploitation of populations of the intertidal bull-kelp *Durvillaea antarctica* (Phaeophyta, Durvilleales) in central Chile. Biol. Cons. 52:205–220.

Castilla, J. C., and L. R. Durán.
1985. Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). Oikos 45:391–399.

Clark, C. W.
1990. Mathematical bioeconomics: the optimal management of renewable resources. John Wiley & Sons, New York, NY, 399 p.

Darcy, G. H.
1983. Synopsis of biological data on the grunts *Haemulon aurolineatum* and *H. plumieri* (Pisces: Haemulidae). U.S. Dep. Commer., NOAA Technical Report NMFS Circular 448, 41 p.

Davis, G. E., and J. W. Dodrill.
1980. Marine parks and sanctuaries for spiny lobster fisheries management. Fish. Bull. 78:979–984.
1989. Recreational fishery and population dynamics of spiny lobster, *Panulirus argus*, in Florida Bay, Everglades National Park, 1977–1980. Bull. Mar. Sci. 44:78–88.

DeMartini, E. D.
1993. Modeling the potential of fishery reserves for managing Pacific coral reef fishes. Fish. Bull. 91:414–427.

Dugan, J. E., and G. E. Davis.
1993. Applications of marine refugia to coastal fisheries management. Can. J. Fish. Aquat. Sci. 50:2029–2042.

Durán, L. R., and J. C. Castilla.
1989. Variation and persistence of the middle rocky intertidal community of central Chile with and without human harvesting. Mar. Biol. 103:555–562.

FAO (Food and Agriculture Organization).
1995. The state of the world fisheries and aquaculture. Food and Agriculture Organization Fisheries Department FAO Fisheries Circular 884, 105 p.

Hay, M. E.
1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? Ecology 65:446–454.

Hay, M. E., and P. R. Taylor.
1985. Competition between herbivorous fishes and urchins on Caribbean reefs. Oecologia 65:591–598.

Hixon, M. A.
1991. Predation as a process structuring coral reef fish communities. *In* P. F. Sale (ed.), The ecology of fishes on coral reefs, p. 475–508. Academic Press, San Diego, CA.

Hixon, M. A., and J. P. Beets.
1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecol. Mono. 63:77–101.

Hixon, M. A., and M. H. Carr.
1997. Synergistic predation, density dependence, and population regulation in marine fish. Science (Wash. D. C.) 277:946–949.

Holland, D. S., and R. J. Brazee.
1996. Marine reserves for fisheries management. Mar. Resource Econ. 11:157–171.

Holland, K. N., C. G. Lowe, and B. M. Wetherbee
1996. Movements and dispersal patterns of blue trevally (*Caranx melampygus*) in a fisheries conservation zone. Fish. Res. 25:279–292.

Holland, K. N., J. D. Peterson, C. G. Lowe, and B. M. Wetherbee.
1993. Movements, distribution and growth rates of the white goatfish *Mulloides flavolineatus* in a fisheries conservation zone. Bull. Mar. Sci. 52:982–992.

Houde, E. D.
1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. Bull. 87:471–495.

Lauck, T., C. W. Clark, M. Mangel, and G. R. Munro.
1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecol. App. 8:S72–78.

Man, A., R. Law, and N. V. C. Polunin.
1995. Role of marine reserves in recruitment to reef fisheries: a metapopulation model. Biol. Cons. 71:197–204.

McAllister, D. E.
1988. Environmental, economic and social costs of coral reef destruction in the Philippines. Galaxea 7:161–178.

McClanahan, T. R., A. T. Kamukuru, N. A. Muthiga, M. Gilagabher Yebio, and D. Obura.
1996. Effect of sea urchin reductions on algae, coral, and fish populations. Cons. Biol. 10:136–154.

McClanahan, T. R., and B. Kaunda-Arara.
1996. Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. Cons. Biol. 10:1187–1199.

McClanahan, T. R., and S. H. Shafir.
1990. Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. Oecologia 83:362–370.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. J. Torres.
1998. Fishing down marine food webs. Science (Wash. D.C.) 279:860–863.

Plan Development Team.
1990. The potential of marine fishery reserves for reef fish management in the U.S. Southern Atlantic. U.S. Dep. Commer., Technical Memorandum NMFS-SEFC-261, 48 p.

Plaut, I.
1993. Sexual maturity, reproductive season and fecundity of the spiny lobster *Panulirus penicillatus* from the Gulf of Eilat (Aqaba), Red Sea. Aust. J. Mar. Freshwater Res. 44:527–535.

Plaut, I., and L. Fishelson.
1991. Population structure and growth in captivity of the spiny lobster *Panulirus penicillatus* from Dahab, Gulf of Aqaba, Red Sea. Mar. Biol. 111:467–472.

Polacheck, T.
1990. Year around closed areas as a management tool. Nat. Resource Model. 4:327–354.

Polunin, N. V. C., and C. M. Roberts (eds.).
1996. Reef fisheries. Chapman and Hall, New York, NY, 495 p.

Quinn, J. F., S. R. Wing, and L. W. Botsford.
1993. Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin *Strongylocentrotus franciscanus*. Am. Zool. 33:537–550.

Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fisheries and Marine Service, Ottowa, 400 p.

Roberts, C. M.
1995. Effects of fishing on the ecosystem structure of coral reefs. Cons. Biol. 9:988–995.
1997. Connectivity and management of Caribbean coral reefs. Science (Wash. D.C.) 278:1454–1457.

Roberts, C. M., W. J. Ballantine, C. D. Buxton, P. Dayton, L. B. Crowder, W. Milon, M. K. Orbach, D. Pauly, and J. Trexler.
1995. Review of the use of marine fishery reserves in the U.S. southeastern Atlantic. U.S. Dep. Commer., NOAA Technical Memorandum NMFS-SEFC-376, 31 p.

Roberts, C. M., and N. V. C. Polunin.
1991. Are marine reserves effective in management of reef fisheries? Rev. Fish Biol. Fish. 1:65–91.
1993. Marine reserves: simple solutions to managing complex fisheries? Ambio 22:363–368.
Rowley, R. J.
1994. Marine reserves in fisheries management. Aquat. Cons. Mar. Freshwater Ecosyst. 4:233–254.
Russ, G.
1985. Effects of protective management on coral reef fishes in the central Philippines. Proceedings of the 5th International Coral Reef Congress 4:219–224,
Russ, G. R., and A. C. Alcala.
1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. Mar. Ecol. Prog. Ser. 132:1–9.
Safina, C.
1993. Bluefin tuna in the West Atlantic: negligent management and the making of an endangered species. Cons. Biol. 7:229–234.
Sladek Nowlis, J., C. and M. Roberts.
1997. You can have your fish and eat it, too: theoretical approaches to marine reserve design. Proceedings of the 8th International Coral Reef Symposium 2:1907-1910, Smithsonian Tropical Research Institute, Panama City, Panama.
Thompson, R., and J. L. Munro.
1983. The biology, ecology and bionomics of the hinds and groupers, Serranidae. *In* J. L. Munro (ed.), Caribbean coral reef fishery resources, p. 59–81. International Council for Living Aquatic Resources Management, Manila.
Wolanski, E., and J. Sarsenski.
1997. Larvae dispersion in coral reefs and mangroves. Am. Sci. 85:236–243.

Appendix

Fecundities

Fecundities were size-specific, but the general form of the equation relating size to fecundity varied from species to species. The specific relationships are listed in Table 1 as r. These r values were set to zero for all classes smaller than the size at maturity.

Larval survival

We used equations developed by Houde (1989) that relate ambient temperature during development to duration of larval stage, daily mortality risk, and probability of surviving through the entire larval stage.

$$D = 952.5\ T^{-1.0752} \quad (1)$$

$$Z = 0.0003149\ T \quad (2)$$

$$N = e^{-Z\,D}, \quad (3)$$

where T = ambient temperature during development, in degrees Celsius;
D = duration of larval stage, in days;
Z = probability of mortality, per day; and
N = probability of surviving through the entire larval stage.

Adult survival

We assumed that newly settled fish experienced density dependence. Thus, instead of surviving at a rate v_i like individuals in other size classes, their survival was weighted by a density-dependent function of the form $e^{-\rho/K}$ where ρ = the population density and K = a measure of carrying capacity arbitrarily set at 1000 due to a lack of information on carrying capacities for the fish we studied. Note that size-class-1 individuals included new recruits that survived and grew as well as old size-class-1 individuals that survived but did not grow to size class 2. Thus, at time t, the densities of size-class-1 individuals in the reserve ($S_{1,t}$) and the fishing area ($F_{1,t}$) are

$$S_{1,t} = v_0 p(0) S_{0,t-1} e^{-S_{0,t-1}/K} + v_1(1-p(1))S_{1,t-1} \quad (4)$$

$$F_{1,t} = v_0 p(0) F_{0,t-1} e^{-F_{0,t-1}/K} + v_1(1-p(1))F_{1,t-1}, \quad (5)$$

where v_x = the density-independent survival rate for individuals in size class x.

Note that the density in the fishing area is decreased later in the program to account for fishing mortality but only for size classes larger than the size at fishery recruitment. Also note that other size classes experience the density-independent survival rate v_x.

Growth

We began with standard von Bertalanffy equations (Ricker, 1975), relating length to age and weight to length (Fig. 2) and categorized them as described by Figure 2. Through algebraic manipulation, we established a formula for $g(B_x)$, the size of an individual projected one year in the future:

$$g(B_x) = e^{-k} B_x + (1 - e^{-k}) L_{inf}. \quad (6)$$

We used this formula to establish the following calculation for $p(x)$, the probability that an individual in size class x grows to size class x+1 by next year.

$$p(x) = \frac{g(B_{x+1}) - B_{x+1}}{g(B_{x+1}) - g(B_x)} = \frac{L_\infty - B_{x+1}}{L_\infty - st - L_0} = \frac{L_\infty - B_{x+1}}{L_\infty - L_1}. \quad (7)$$

Net efficiency of a survey trawl for snow crab, *Chionoecetes opilio*, and Tanner crab, *C. bairdi*

David A. Somerton
Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE
Seattle, Washington 98125
E-mail address: david.somerton@noaa.gov

Robert S. Otto
Kodiak Laboratory
Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
PO Box 1638
Kodiak, Alaska 99615

Abstract.–Snow crab (*Chionoecetes opilio*) and Tanner crab (*C. bairdi*) fisheries in the eastern Bering Sea are managed by using swept-area estimates of biomass based on an annual survey conducted with a 83-112 eastern bottom trawl. Estimates of net efficiency (i.e. the capture probability of crab that occur between the wing-tips of the trawl net) are needed to correct the biomass estimates for any size selectivity by the trawl. Data on net efficiency were obtained experimentally by attaching an auxiliary net beneath the trawl net to capture crab escaping under the trawl footrope. Net efficiency is then the quotient of the trawl catch divided by the combined catch of the trawl and auxiliary nets. Mathematical models of the relationship between net efficiency and carapace width were formulated and fitted to the experimental data. Net efficiency for both species first decreased with increasing carapace width until a minimum efficiency was reached near 50 mm carapace width. At larger sizes, efficiency increased asymptotically with carapace width. Net efficiency for mature female Tanner crab was lower (0.47) than for males and immature females combined (0.72) at the same mean carapace width as mature females (66–107 mm). Net efficiency did not differ between morphologically mature and immature male Tanner crabs of the same carapace width.

Manuscript accepted 3 November 1998.
Fish. Bull. 97:617–625 (1999).

The commercial fisheries for snow crab (*Chionoecetes opilio*) and Tanner crab (*C. bairdi*) in the eastern Bering Sea are managed by using swept-area estimates of biomass (Alverson and Pereyra, 1969) provided by an annual Alaska Fisheries Science Center (AFSC) bottom trawl survey. In addition to catch and swept-area data, such biomass estimates require a value for the sampling efficiency of the trawl[1] (i.e. the proportion of animals that are captured within the area spanned by the trawl doors; Dickson, 1993a). Trawl efficiency can be considered as a function of sweep efficiency (the proportion of animals within the path of the doors, bridles, and sweeps that are herded into the net path) and net efficiency (the proportion of animals that are captured within the path of the trawl net; Dickson, 1993a). For snow and Tanner crabs, owing to a lack of any contradictory evidence, sweep efficiency was assumed to be zero and net efficiency was assumed to be unity. The assumption of zero sweep efficiency has been subsequently supported by experiments on herding,[2] but the assumption of complete net efficiency has been contradicted by studies in which low-light video cameras have documented that even large male crabs could often escape under the footrope.[3] Such observations prompted us to experimentally estimate net efficiency of the 83-112 eastern trawl, the trawl used for the eastern Bering Sea surveys.

Previous studies of net efficiency, which were focused at various species of groundfish, indicated that efficiency generally increases with body size (Engås and Godø, 1989; Walsh, 1992). For snow and Tanner crab, however, biological attributes other than size could also influence efficiency. For example, mature males have longer legs and thicker chelae, in relation to their carapace width, than either mature females or immature males. Not only could the difference in body shape result in differing net efficiency, differ-

[1] Throughout this paper we will refer to the trawl as an entire fishing gear comprising the net, bridles, and doors.

[2] Somerton, D. A., and P. T. Munro. 1998. Estimating the sweep efficiency of a bottom trawl. Manuscript in preparation.

[3] Munro, P. T. 1998. Alaska Fisheries Science Center, 7600 Sand Point Way NE Seattle, WA. Unpubl. data.

ences in behavior between sexes or between mature and immature individuals but could also lead to differences in efficiency. Of particular concern is a possible difference in net efficiency between mature and immature males because such a difference could lead to a bias in the estimates of the carapace width at maturity and thereby affect commercial minimum width regulations.

We estimated net efficiency with an experimental approach pioneered by Engås and Godø (1989) that uses an auxiliary net attached beneath the trawl net to capture crab escaping under the footrope. If the auxiliary net spans the fishing width of the trawl net, from wing-tip to wing-tip, and captures everything passing beneath the footrope, then efficiency is estimated as the quotient of the trawl catch divided by the total catch of both the trawl and auxiliary net (Walsh, 1992; Dickson 1993b). The crux of such an experiment is then to design an auxiliary net with a footrope that exerts sufficient bottom contact to capture everything passing beneath the trawl footrope without causing enough added drag to alter the fishing efficiency of the trawl. Unlike the trawls examined in the studies of Engås and Godø(1989) and Walsh (1992), the 83-112 trawl lacks bobbins or rollers on the footrope and instead has a footrope consisting of a simple, rubber-wrapped cable. This difference in trawl design required several distinct differences in the design of the auxiliary net. In this paper we examine the application of this auxiliary net to estimate the efficiency of the 83-112 eastern trawl for snow and Tanner crabs.

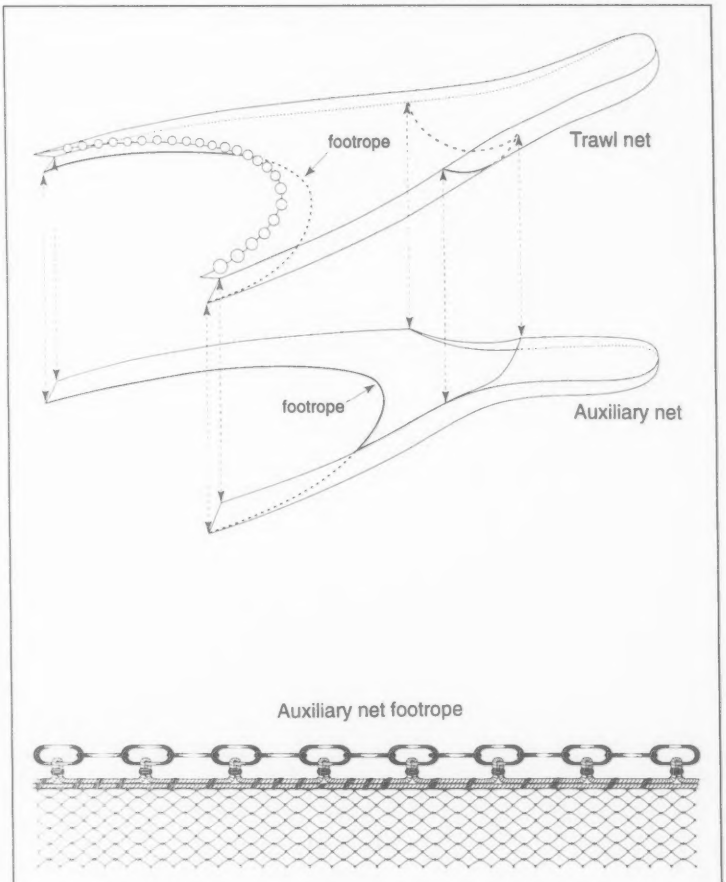


Figure 1

The 83-112 eastern trawl net and the auxilary net. The dashed lines show the corresponding attachment points on both the trawl and auxilary nets, but the two nets are sewed together along the entire edge of the auxilary net.

Materials and methods

Description of the trawl and auxiliary net

The 83-112 eastern trawl is a two-seam trawl with a 25.3-m headrope and a 34.1-m footrope consisting of a simple rubber-wrapped cable intended to remain in close contact with a smooth bottom (Fig. 1; see Armistead and Nichol, 1993, for a detailed net plan). The trawl is towed behind 1.8 × 2.7 m steel "V" doors weighing 816 kg each, which are connected to each wing with two 55-m bridles. Wing and throat sections of the net are made of 10.1-cm (stretched measure) nylon mesh, the intermediate section is made of 8.9-cm mesh and the codend is made with a double layer of 8.9-cm mesh lined with 3.1-cm mesh.

The auxiliary net was hung beneath the trawl net, attached at the wing tips and along the top of the wings (Fig. 1). Unlike the auxiliary net designs of Engås and Godø (1989) and Walsh (1992), our auxiliary net lacked a headrope, used the belly mesh of the trawl as the top panel, and had a single codend rather than three separate codends. The mesh used in the auxiliary net was the same as that for the trawl, but the footrope was longer (38.2 m) and was constructed of 16-mm long-link steel chain intended to be sufficiently heavy to excavate buried crab. An

additional feature of the auxiliary net was that the footrope was not attached anywhere along the length of the trawl footrope but instead joined it only at the wing tips. The auxiliary net footrope was intended to be positioned 2–3 m behind the trawl footrope along the center line of the trawl, but this position was not verified in the field.

Description of the experiment

The net efficiency experiment was conducted aboard a chartered 40-m stern trawler (FV *Arcturus*), from 20 July 1997 to 8 August 1997, immediately following completion of the annual AFSC trawl survey of the eastern Bering Sea. The experimental site was located east of the Pribilof Islands (57°11.4'N, 166°26.5'W) at depths between 75 and 90 m on a smooth bottom.

All hauls were made by using the same trawling procedure and towing speed (3 knots) as those used during the AFSC survey but tow duration (15 min) was only one half of the standard. Trawl net width, from wing-tip to wing-tip, was measured on all hauls with a SCANMAR net mensuration system.

The experiment began with test hauls of both the standard trawl and the trawl with the attached auxiliary net (experimental trawl) to determine if trawl performance was altered by the auxiliary net. All test hauls were conducted with the codends left open and with a video camera attached so that the trawl footrope near its center could be viewed. After three hauls of the experimental trawl, it became evident that the additional drag of the auxiliary net resulted in a reduction in the opening width of the trawl net. To help correct this problem, the bridles were shortened from the standard length of 55 m to 28 m. The shorter bridles were used for the remainder or the experiment.

All crab were removed from each catch and sorted into two groups: mature females, which were recognized by the presence of an enlarged abdomen, and all other crab. For simplicity, we will refer to the group "all other crab" as "mixed sexes." Carapace width, to the nearest 1 mm, was measured with vernier calipers on all individuals. On some hauls, randomly selected male Tanner crab were subsequently removed from the mixed sexes baskets and measured for both carapace width and chela height (right hand side) to allow determination of morphometric maturity.

Estimating net efficiency

Net efficiency (E_n) typically is an increasing function of body size (Engås and Godø, 1989; Walsh, 1992). To provide more flexibility, however, we modeled the relationship between net efficiency and carapace width as a function of two width-dependent processes: the probability of entering the net at the footrope (P_f) and the probability of entering the net through the belly mesh after escaping under the footrope (P_b). Algebraically this relationship can be expressed as

$$E_n = P_f + (1 - P_f)P_b. \quad (1)$$

The probability of entering the trawl at the footrope, was described with a three-parameter logistic function:

$$P_f = \frac{a}{1 + be^{(-cw)}}, \quad (2)$$

where a, b, and c = parameters; and
w = carapace width.

This function was chosen because it provides predicted values of P_f that increase with w asymptotically to a value of a and permits cases where efficiency is less than unity even at the largest body sizes. The probability of entering the trawl through the belly mesh was described by a two-parameter decreasing logistic function:

$$P_b = 1 - \frac{1}{1 + de^{(-fw)}}, \quad (3)$$

where d and f = parameters.

This function was chosen because it provides predicted values of P_b that decrease with w asymptotically to a value of zero.

The model resulting from substituting Equations 2 and 3 into Equation 1 was fitted to values of net efficiency for each 1-mm increment of carapace width by using a maximum likelihood procedure where the number of crab captured in the trawl net at each carapace width was described by a binomial random variable (Millar, 1992). The parameters of the model were estimated by minimizing the negative logarithm of the likelihood function:

$$L = -\sum_w \left(n_w \log E_{n,w} + (N_w - n_w)\log(1 - E_{n,w}) \right), \quad (4)$$

where, at each value of carapace width w,

n_w = the number of crab captured in the trawl net;
N_w = the total number of crab in the trawl and auxiliary nets combined; and
$E_{n,w}$ = the net efficiency.

N_w and n_w were calculated by pooling together the data from all good tows. For mature female crab, a simplified model consisting of only the P_f term was fitted to data because the smallest mature females were too large to fit through the belly meshes of the trawl net. In both cases, the models were fitted to the data by using the S+ function MS (Venables and Ripley, 1994).

The 95% confidence intervals for $E_{n,w}$ were estimated by using a bootstrap analysis (Efron and Tibshirani, 1993) which considered between-haul variability but ignored within-haul binomial variability which is relatively small. Each bootstrap estimate of $E_{n,w}$ was calculated by randomly sampling individual hauls with replacement from the original data, then by fitting the model to the data from the chosen hauls pooled together. After replicating the bootstrap process 240 times, values of $E_{n,w}$ at each increment of carapace width were then ranked. The upper and lower confidence intervals were chosen as the values of $E_{n,w}$ ranked 7th and 234th at each width increment.

Two tests of model form were conducted. First, to determine if the P_b term was a significant contribution to the model, the goodness of fit of the model, including both the P_f and P_b terms (five parameters), was compared to that of a model including only the P_f term (three parameters) by using a likelihood ratio test (pages 153–155 in Hilborn and Mangel, 1997). Second, to determine if the models for mixed sexes differed between crab species, the summed likelihoods of the model fit to each species were compared with the likelihood from a model fitted to the combined data for both species by using a likelihood ratio test. For both tests, significance of the likelihood ratio was evaluated by using a chi square statistic with degrees of freedom equal to the difference in parameters between the models being tested (Hilborn and Mangel, 1997).

In addition to the tests on model form, two tests were also conducted for differences in net efficiency between biological subgroups of Tanner crab. First, a test was conducted to determine whether net efficiency differs between mature females and mixed sexes restricted to the same range of carapace width as mature females. Because of the restricted range of carapace widths, we assumed that net efficiency could be modeled as a simple logistic function of carapace width and sex. This model was fitted by using the S+ function GLM (Venables and Ripley, 1994). Second, a test was conducted to determine whether net efficiency for mature male Tanner crab differed from that for immature male Tanner crab of equal size. Male crab were categorized as either immature or mature on the basis of height of their chela in relation to their carapace width by using the computer technique of Somerton (1980). Both categories were then restricted to a common range of carapace width that was spanned by the smallest mature and the largest immature individuals. Net efficiency was then modeled as a function of maturity and carapace width by using logistic regression. Significance of the sex term in the first test and the maturity term in the second test were assessed with analysis of deviance (page 186 in Venables and Ripley, 1994). When a term was significant, the resulting model was evaluated to predict net efficiency for each biological class at the midpoint of the carapace width interval examined.

Results

Effect of the auxiliary net on trawl performance

The attachment of the auxiliary net to the trawl net resulted in a decrease in wing spread, presumably from increased drag on the bottom. During the testing phase when the codends of both the trawl and auxiliary nets remained open, average wing spread for hauls with standard 55-m bridles was 14.3 m (n=3), considerably less than the mean width of the standard net (mean=17.0, n=29) used during the preceding survey hauls with the same length of towing cable. To help compensate for the additional drag of the auxiliary net, we shortened the bridles to 28 m. This increased average wing spread to 15.4 m (n=4). When the codends were closed, however, the auxiliary net rapidly filled with epibenthic fauna, especially brittlestars, resulting in a progressive narrowing of the wing spread by as much as 3 m over the duration of a haul. After seven attempts at trawling in the initial study area, we were forced to locate a new study area with a lower abundance of brittlestars. The progressive narrowing was nearly eliminated by the change of sampling site, but the mean wing spread during the remainder of the experimental hauls (mean=15.9, n=24) was still significantly less (t-test, t=5.18, P<0.001) than the standard net.

Although the wing spread was less during the experiment than during the AFSC survey, the departure from the standard width may not have been great enough to affect footrope contact with the bottom. Footrope contact at the center of the trawl was evaluated by using a video camera for three tows of the standard trawl (mean width=17.5 m), three tows of the experimental trawl with standard bridles (mean width=14.3 m), and three tows of the experimental trawl with short bridles (mean width=15.3 m). In all cases, the footrope in the bosom of the trawl did not contact the bottom, as evidenced by the lack of mud clouds behind the footrope, but instead

skimmed over the bottom at an estimated height of 1–2 cm. No difference in the proximity of the footrope to the bottom could be visually detected among the three trawl configurations. Because the range in wing spread among the three configurations was greater than the difference between the survey average and the experiment average, it is likely that the addition of the auxiliary net did not alter the contact of the footrope in the center of the trawl where most of the escapement usually occurs (Walsh, 1992).

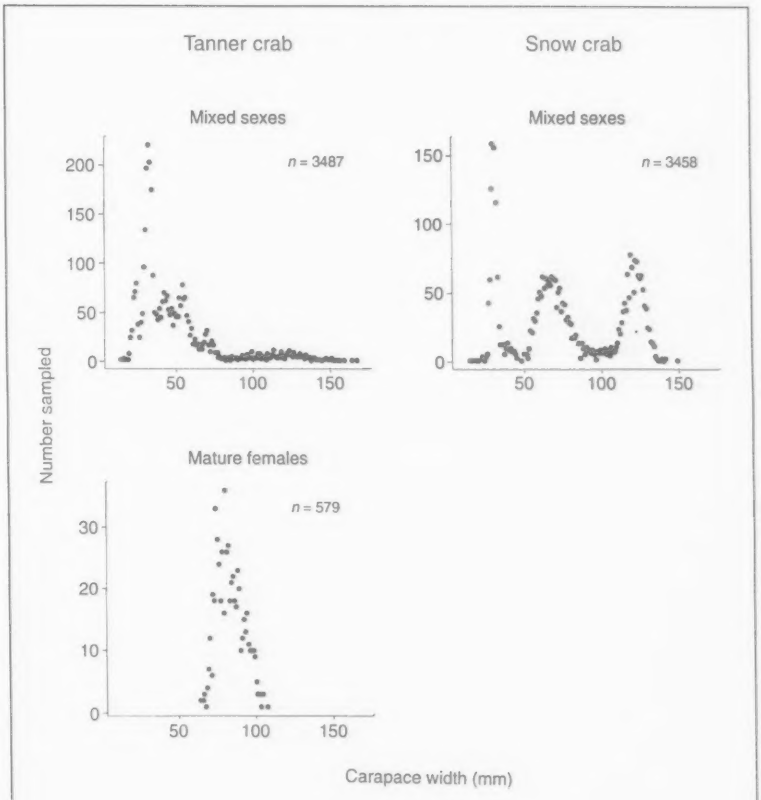


Figure 2

Carapace-width frequency distributions for the mixed sexes of snow crab (*Chionoecetes opilio*) and for the mixed sexes and mature females of Tanner crab (*C. bairdi*).

Description of the data

Thirty-one hauls of the experimental trawl were completed, but the data from the first seven were not used in subsequent analysis because of unusual trawl performance (the narrowing of wing spread associated with large catches of epibenthic fauna in the auxiliary net). For snow crab, width measurements were collected from 3458 individuals from the mixed sexes category, but from only three individuals from the mature female category. The low sample size for mature females prevented further analysis. Carapace-width frequency distributions indicated that a broad range of carapace widths was sampled, but the observations were concentrated in three carapace width modes (Fig. 2). For Tanner crab, width measurements were collected from 3487 individuals from the mixed sexes category, and from 579 individuals from the mature female category. Sampling for both categories covered a broad range of carapace widths, but for the mixed sexes category the observations were concentrated at smaller carapace widths. Plots of net efficiency against carapace width (Fig. 3) for the mixed sexes groups of both species showed an initial decline with increasing width until a minimum in net efficiency was reached in the range of 40–50 mm, then a steady increase as carapace width increased. For mature female Tanner crab, the narrow range of carapace widths and the large variance in net efficiency obscured any obvious change in net efficiency with carapace width (Fig. 3).

The fitted models

For the mixed-sexes category of both species, the models that included both the P_f and P_b terms fitted the data significantly better than the models with only the P_f term (Tanner crab, likelihood ratio=189.7, $P<0.001$; snow crab, likelihood ratio=60.5, $P<0.001$). This indicates that the apparent increase in net efficiency at small sizes is statistically detectable. Likewise, the separate-species model fitted the net efficiency data significantly better than did the combined species model (likelihood ratio=85.5, $P<0.001$). This indicates that the change in net efficiency with width differs between species. Plots of the fitted models (Fig. 3) indicated that the predicted values of P_b decline rapidly with increasing carapace width and become negligible at about 50 mm for Tanner crab and 60 mm for snow crab. For mature female Tanner crab, the model considering only the P_f term fitted the data significantly better than did the sample mean (likeli-

hood ratio=4.27, P=0.014), indicating that net efficiency increased significantly over the narrow width range of mature females (66–107 mm). Estimated parameter values for the fitted models are shown in Table 1.

For male Tanner crab, net efficiency for mature males (0.82, n=99) was not significantly different (analysis of deviance, P=0.47) than for immature males (0.81, n=39) at the center of the width interval spanned by the largest immature and the smallest mature individuals. This indicates that mature males are not preferentially selected by the survey trawl. For mature female Tanner crab, net efficiency (0.47, n=578) was significantly different (analysis of deviance, P<0.001) than the value for the mixed-sex group (0.72, n=441) at the midpoint of the mature female size range. This finding indicates that net efficiency was substantially less for mature females than for the mixed-sexes category (combined sexes excluding mature females).

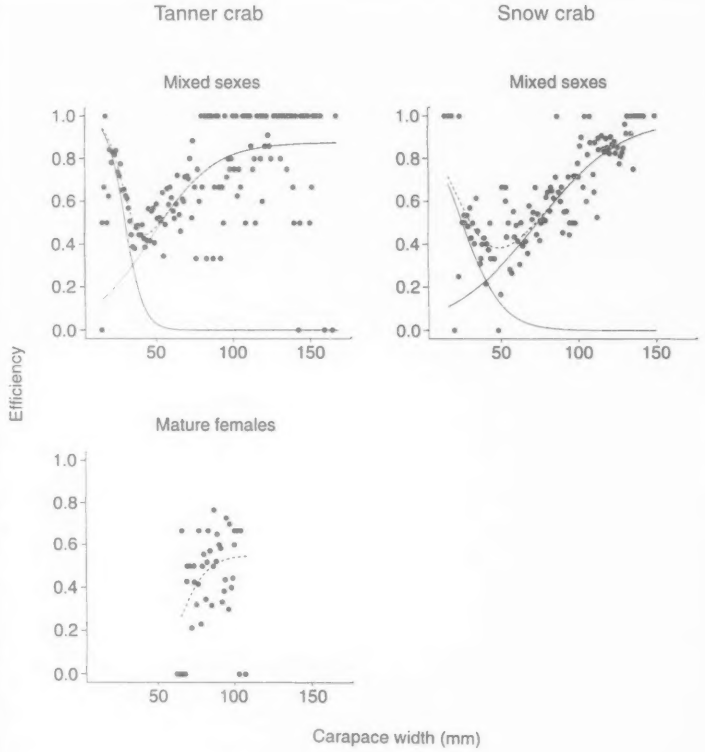


Figure 3

Values of net efficiency by 1-mm intervals of carapace width (filled circles) and the fitted model (dashed line). Also shown for the mixed sexes categories of both species are the two model components, P_f (solid line ascending to the right) and P_b (solid line decending to the right).

Discussion

Experimental trawl performance

Net efficiency estimates from auxiliary net experiments are potentially subject to two sources of bias. First, bias may result if the efficiency of the experimental trawl differs from that of the standard trawl. Of particular concern is any distortion of trawl geometry caused by the auxiliary net that changes the position of the footrope and fishing line in relation to the bottom. In our case, trawl net width was reduced by the increased drag of the auxiliary net. We attempted to compensate for this increased drag by reducing the bridles to one half of their standard length, but the resulting trawl net width was still approximately one meter less than the standard. The decreased trawl net width, however, apparently did not alter the proximity of the footrope to the bottom because our video observations did not reveal any conspicuous differences between the standard and experimental trawls. Although these observations were confined to the center of the footrope, previous video observations of the 83-112 trawl indicated that the center of the footrope tends to have lighter bottom contact than the wings and is therefore the area most likely to be impacted by the auxiliary net.

Second, bias may result if the experimental trawl cannot sample all habitats sampled by the standard trawl. To be effective, the footrope of an auxiliary net must fish harder on the bottom than the footrope of a trawl net. Consequently, the auxiliary net is more prone to damage from snagging on rocks and from filling with epibenthos and debris. Although, in our case, the chain footrope on the auxiliary net may have been effective at excavating buried crab, it also resulted in large catches of epibenthic fauna which, in turn, aggravated the problem of narrowed trawl width. We reduced the narrowing by moving the experiment to a location lacking high quantities of epibenthos, but by doing so we

Table 1

Parameter estimates of the fitted models for the mixed sexes of snow crab (*Chionoecetes opilio*) and the mixed sexes and mature female categories of Tanner crab (*C. bairdi*).

Parameter estimates	Snow crab mixed sexes	Tanner crab mixed sexes	Tanner crab mature females
a	0.9894	0.8743	0.5500
b	14.49	10.95	2003.0
c	0.0366	0.0504	0.116
d	7.905	185.9	
f	0.0810	0.1742	

excluded from consideration a type of habitat occupied by snow and Tanner crabs. Thus the net efficiency estimates we obtained may not be representative of the entire area covered by the survey.

Model form

The form of the model that we chose to describe the relation between net efficiency and carapace width included a term (P_f) that increases with width to account for entry into the trawl over the footrope and another term (P_b) that decreases with width to account for entry of crabs through the belly meshes of the trawl after they have passed under the footrope. The model with both P_f and P_b terms fitted the mixed-sexes data of both species significantly better than the model with only a P_f term, confirming the significance of the apparent increase in net efficiency with decreasing size at carapace widths less than 50 mm. However, we have been unable to verify that the increased efficiency is indeed due to the entry of small crab through the belly meshes. Regardless of the mechanism, the important question is whether the increase in net efficiency at small size is a normal property of the 83-112 trawl or an artifact of the experiment. We attempted to answer this question by comparing the width distributions of crab captured in the trawl net of the experimental trawl with those captured in the standard trawl at the same or nearby stations during the survey preceding the experiment, but patchiness and small sample sizes made the results equivocal.

In light of this uncertainty, the composite form of the model is advantageous because it allows separation of the P_f and P_b effects. For example, if further research reveals that the increase in efficiency at small size is associated with the attachment of the auxiliary trawl, then an estimate of net efficiency without this effect can be obtained by deleting the P_b term and by evaluating the reduced model with the parameters from the fit of the complete model (Table 1). For this reason, the bootstrapped confidence intervals we provide (Fig. 4) are computed two ways, by evaluating the full model and by fitting the full model but evaluating only the P_f term. However, because the P_b term decreases rapidly with carapace width, the full and reduced models predict nearly identical values of net efficiency at carapace widths above 50–60 mm, which includes the mature and commercial width ranges for both species.

Efficiency differences between biological subgroups

The survey trawl is less efficient for mature female Tanner crab than for the mixed-sexes group over the same range of carapace width. Since the mixed-sexes group is primarily male at these sizes, the difference in efficiency is likely due to between sex differences in both morphological features and behavior. Male Tanner crab have longer legs, in relation to their carapace width, than do mature females. Not only does this increase their effective size in relation to the trawl mesh but also may result in their bodies being held higher off the bottom in relation to the footrope. In addition, male Tanner crab may be caught more efficiently because they are less sedentary than females and less prone to bury themselves.[4]

The survey trawl efficiency does not differ between mature and immature male Tanner crab. We were concerned that mature males, which have larger claws and are perhaps more active than immature males, might be preferentially selected. If such selection did occur, it would lead to an underestimate of the carapace width at maturity which is used in establishing minimum width limits for the commercial fishery. Apparently such preferential selection of mature males does not occur.

In the foregoing, we estimated values of net efficiency or the capture probability of crab that occur between the wing-tips of the trawl net. For stock assessment purposes, however, it may be more convenient to consider these values expressed as trawl efficiency or the capture probability of crab that occur between the trawl doors. In situations where the bridles herd animals into the path of the trawl, further experiments to estimate sweep efficiency would be required to estimate trawl efficiency (Dickson, 1993a, 1993b). However, experiments on herding snow crab indicate that this species is not herded by the bridles of the 83-112 eastern trawl.[2] Thus, trawl efficiency can be estimated simply by multiplying net efficiency by the quotient of the net width divided by the door width (i.e. 0.30).[2]

[4] Stevens, B. 1998. Kodiak Laboratory, National Marine Fisheries, P.O. Box 1638, Kodiak, AK. Personnal commun.

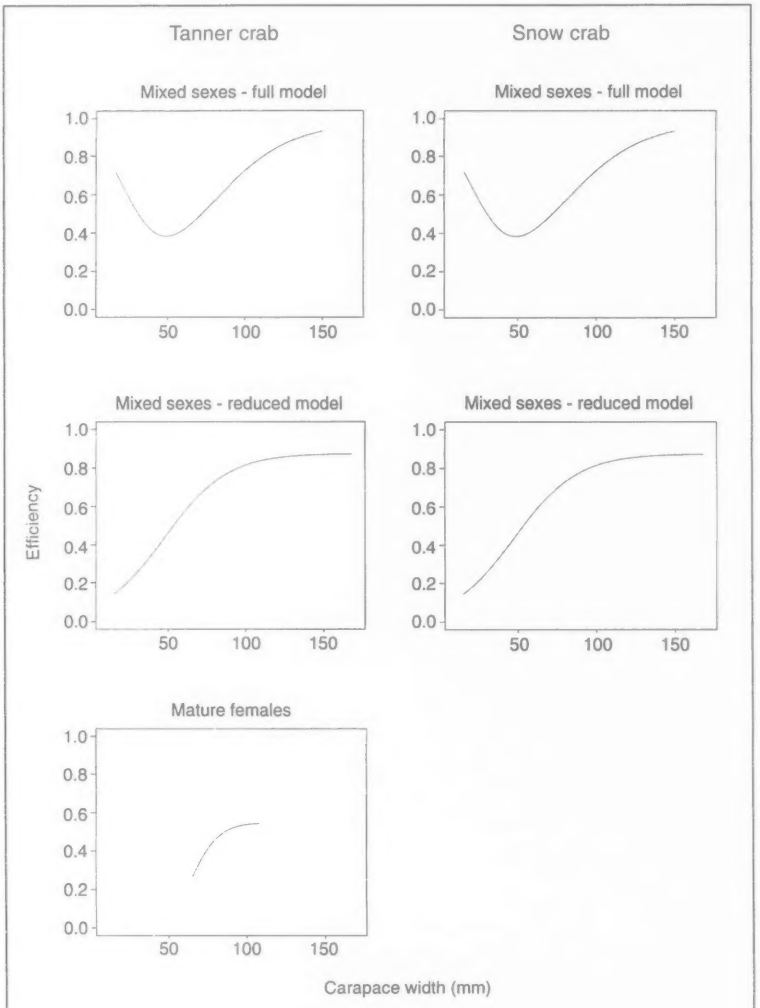


Figure 4

Fitted model and 95% bootstrap confidence intervals about the predicted value of net efficiency. For the mixed-sexes categories of both crab species, values of net efficiency are predicted in two distinct ways after fitting the full model (Equation 1) to the data. First, net efficiency was predicted by evaluating both P_f and P_b terms of the model (top row), based on the assumption that the entry of small crabs into the trawl net through the belly mesh occurs during normal trawl operations. Second, net efficiency was predicted by evaluating only the P_f term (i.e. setting P_b=0), based on the assumption that the entry of small crab through the belly mesh was an expermental artifact caused by adding the auxiliary trawl (second row).

Acknowledgments

We thank J. Ianelli, S. Syrjala, and D. Pengilly for reviewing the manuscript and offering helpful comments, P. Munro for designing the auxiliary trawl, and D. Nichol and J. Hoff for supervising the field experiment.

Literature cited

Alverson, D. L., and W. T. Pereyra.
1969. Demersal fish explorations in the Northeastern Pacific Ocean—an evaluation of exploratory fishing methods and analytical approaches to stock size and yield forecasts. J. Fish. Res. Board Canada 26:1985–2001.

Armistead, C. E.. and D. G. Nichol.
1993. 1990 bottom trawl survey of the eastern Bering Sea continental shelf. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-7, 190p.

Dickson, W.
1993a. Estimation of the capture efficiency of trawl gear. I: development of a theoretical model. Fish. Res. 16:239–253.
1993b. Estimation of the capture efficiency of trawl gear. II: testing a theoretical model. Fish. Res. 16:255–272.

Efron, B., and R. Tibshirani.
1993. An introduction to the bootstrap. Chapman and Hall, New York, NY, 436p.

Engås, A., and O. R. Godø.
1989. Escape of fish under the fishing line of a Norwegian sampling trawl and its influence on survey results. J. Cons. Int. Explor. Mer 45:269–276.

Hilborn, R., and M. Mangel.
1997. The ecological detective: confronting models with data. Princeton Univ. Press, Princeton, NJ, 315 p.

Millar, R. B.
1992. Estimating the size-selectivity of fishing gear by conditioning on the total catch. J. Am. Stat. Assoc. 87:962–968.

Somerton, D. A.
1980. A computer technique for estimating the size of sexual maturity in crabs. Can. J. Fish. Aquat. Sci. 37:1488–1494.

Venables, W. N., and B. D. Ripley.
1994. Modern applied statistics with S-plus. Springer-Verlag, New York, NY, 462 p.

Walsh, S. J.
1992. Size-dependent selection at the footgear of a groundfish survey trawl. N. Am. J. Fish. Man. 12:625–633.

Nursery habitats, growth rates, and seasonality of age-0 red snapper, *Lutjanus campechanus*, in the northeast Gulf of Mexico*

Stephen T. Szedlmayer

Joseph Conti

Marine Fish Laboratory
Department of Fisheries and Allied Aquacultures
Auburn University
8300 State Highway 104
Fairhope, Alabama 36532

E-mail address (for S. T. Szedlmayer): sszedlma@acesag.auburn.edu

Abstract.—We sampled inner shelf habitat in the northeast Gulf of Mexico, for age-0 red snapper, *Lutjanus campechanus*, to estimate growth rates and seasonality, as well as to identify nursery habitats. We collected 7507 age-0 red snapper in 1994 and 1995, from 536 10-min trawl tows. Red snapper first settled to benthic habitat in June after reaching 17.4 mm standard length (age=26 d). In both years, catch per unit of effort (CPUE=number/10-min tow) peaked July through September, then declined in the fall as fish were leaving the habitat before winter. Most fish (80–81%) were caught at one location, 13 km south of Mobile Bay, Alabama. At this location in 1995, the August CPUE ±SE (712 ±243) far exceeded all previous estimates. Based on otolith microincrements, hatching-date frequencies showed distinct cohorts in June and July 1994 and May and June 1995. Growth rates for the June (0.77 mm/d) and July (0.71 mm/d) cohorts in 1994 were significantly faster compared with growth rates for May (0.51 mm/d) and June (0.67 mm/d) cohorts in 1995. Density-dependent mechanisms may be operating with faster growth rates and lower CPUEs in 1994, compared with slower growth rates and higher CPUEs in 1995. However, environmental constraints may also be operating, as indicated by the slow growth rate of the May 1995 cohort that probably resulted from colder temperatures. Newly settled red snapper were aggregated on the inner shelf, at a particular location and time period. These concentrations indicated an important nursery habitat just south of Mobile Bay, Alabama, from July through September.

Manuscript accepted 20 August 1998.
Fish. Bull. 97:626–635 (1999).

To enhance survival some fishes spawn many times within a given season (Lambert and Ware, 1984). This strategy may produce several distinct cohorts at the juvenile stage within that season (Szedlmayer et al., 1990), and individual cohorts may have an advantage over others owing to biotic and abiotic environmental factors (Miranda and Hubbard, 1994). For example, faster growth may increase survival because fish grow past size-specific predators more quickly than slower growing fish (Houde, 1987; Sogard, 1997).

Red snapper, *Lutjanus campechanus*, have an extended spawning season (Moseley, 1966; Collins et al., 1996) and within-year variations in early life stages might be expected, but information on the age-0 juvenile stage of red snapper is sparse, especially at first settlement. Baughman (1943) suggested that immature fish came close to shore, but this observation was based on only five juvenile red snapper. Ogren and Brusher (1977) indicated inshore nursery areas for age-0 red snapper in the deeper portions of St. Andrew's Bay, Florida, but catch rates were low—a total of 62 fish in 312 10-min trawl tows. Bradley and Bryan (1975) caught young red snapper during summer months and suggested that juvenile red snapper sought deeper water as they grew older, albeit their catch rates were also low, with a maximum of 10 fish/10-min tow. Holt and Arnold (1982) showed a bimodal size distribution in juvenile red snapper from June through December, but this pattern was derived from separate year classes, where red snapper reached 110–130 mm during their first year, 220–230 mm during their second year. Age-0 red snapper were conspicuously absent from that study in July, and only 26 age-0 red snapper were collected in three years of August samples. Szedlmayer and Shipp (1994) reported a catch rate for age-0 red snapper in July 1991 that exceeded all previous studies (130 fish/10-min tow), but their effort was low with only 17 trawl tows in July, August, and October.

Despite these previous efforts, no study has specifically targeted age-0 red snapper just after settlement. Thus, we suspected that the primary nursery habitats used by first settlers had not been adequately sampled. In the present study we examine the early life stage of red snapper just after settlement. We determine growth rates, distribution, seasonality, and

* Contribution 8996031, Auburn University Alabama Agriculture Experiment Station, Auburn University, Fairhope, AL 36532.

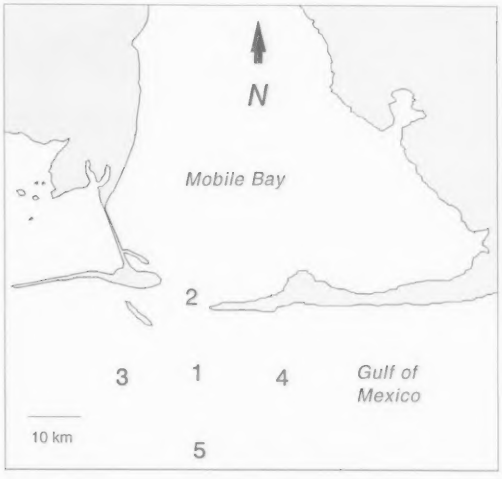


Figure 1
Map of station locations in the northeast Gulf of Mexico.

abundance; and identify multiple cohorts and primary nursery areas for this species.

Materials and methods

Age-0 red snapper were collected 0–26 km south of Mobile Bay, Alabama. Fish were sampled by trawl (7.62-m head rope, 2.54-cm mesh, 2-mm codend mesh). Five 10-min tows were taken every two weeks, at five fixed stations, from June 1994 through January 1995, and from June 1995 through January 1996 (Fig. 1). Sampling periods were sometimes longer owing to poor weather.

All trawl tows were made with a 6:1 ratio of towing cable length to depth, and tow speeds of 40 to 80 m/min. Bottom dissolved oxygen, salinity, and temperature were recorded with a Hydrolab Surveyor II. We did not sample in May but were able to plot temperature data measured at 1 m depth, for May through December, from a NOAA buoy moored 70 km west of the sites. Sediment samples were collected by SCUBA divers and examined by grain size analysis (Holme and McIntyre, 1971).

All age-0 red snapper were stored on ice in the field and later frozen in the laboratory. Fish were thawed, weighed to the nearest 0.01 g with an Ohaus balance, and measured with a caliper to the nearest 0.1 mm standard length (SL).

Sagittal otoliths were removed from all age-0 red snapper and mounted in epoxy (Spurr, 1969). Left and right sagittal otoliths were assumed to be identical; only one otolith was used to estimate age from a particular fish. Otoliths mounted in epoxy were first cut with a Buehler diamond blade saw, then mounted on glass slides with Crystalbond thermoplastic cement, and ground on both sides in the transverse plane to the primordium, on 400 and 600 grit wet-dry sand paper. Type A alumina powder (0.3 μm) and Buehler polishing cloth were used for final otolith preparations (Secor et al., 1991).

Microincrements of otoliths were counted from the primordium to the margin, along the sulcus ridge, in the transverse plane. We made all counts at 750× magnification, using a Sony GVM video monitor, a Sony CCD video camera, and an Olympus BH2 light microscope.

Two independent blind counts were made on each otolith. If the two independent counts were within 10% of each other, their mean value was used to estimate age. If the two counts differed by >10%, a third blind count was made. The means of the two closest counts were then used to estimate ages. If counts still differed by >10 % after three counts, the otolith was rejected.

Age of each fish was subtracted from date of capture for hatching-date estimations. Hatching-date histograms were plotted after applying a three-day moving average for each year, and local minima were used to separate cohorts (Szedlmayer et al., 1991). A significance level of ≤0.05 was used for all statistical analysis. Catch per unit of effort (CPUE=mean number/10-min tow) was estimated for each sample date and station. Prior to analysis CPUEs were $\log(x+1)$ base-10 transformed. Two-way analysis of variance (ANOVA) was used to test for significant differences in mean CPUEs and mean SLs among dates and stations. Waller-Duncan's multiple comparison test was used to show specific differences detected by the ANOVAs.

Growth rates were estimated by linear regression of SL on collection date, and SL on age from otolith microincrement counts. Analysis of covariance (ANCOVA), Student's t-test, and Tukey's multiple comparison test were used to compare estimated growth rates (Zar, 1984).

Results

Salinity ranged from 30.5 to 35.4 ppt, dissolved oxygen from 3.7 to 7.9 ppm in 1994. Temperature increased from 22°C in June to a peak of 29°C in August, then decreased to 17°C by January 1995. The temperature (26°C) in early June 1995 was higher compared with the previous year, stayed near this level through July, increased to 30°C in September, then decreased in the fall (Fig. 2). Temperature data from the NOAA buoy indicated that temperatures

were probably colder in May of both years at the sample sites (Fig. 2). Temperature, salinity, and dissolved oxygen were similar among stations (Table 1). Visual observations of debris in trawl samples indicated shell deposits at station 1 that were not apparent at other stations. Grain size analysis indicated similar sediments between stations 1 and 5, and between stations 2 and 4, whereas station 3 had a significantly higher silt-clay fraction compared with all other stations (ANOVA, $P \leq 0.05$; Table 1).

From these nursery habitats, we collected 7507 age-0 red snapper from 536 10-min trawl tows in 1994 and 1995. Significantly more fish were collected in 1995 than in 1994 (ANOVA, $P \leq 0.05$; Fig. 3). Age-0 red snapper first settled to these habitats in late June, showed highest abundance July through September, then steadily declined in the fall of both years (ANOVA, $P \leq 0.05$; Fig. 3). Most fish, 80–81%, were collected at station 1 (ANOVA, $P \leq 0.05$; Fig. 4). At station 1, significantly higher peaks in CPUE ±SE for 1994, were 63.6 ±8.9 in July, 60.8 ±26.2 in August, and 40.3 ±13.4 in September (ANOVA, $P \leq 0.05$). In late August 1995 at station 1, we observed a CPUE (712 ±243) that far exceeded all previous estimates from this study or any previous study. Other significant peaks in CPUE for 1995 at station 1 were 76.2 ±21.4 in mid-August, and 81.4 5.0 in mid-September (ANOVA, $P \leq 0.05$).

Age-0 red snapper ranged from 17.8 to 124.4 mm SL. Fish first settled from the plankton after they reached 17.8 mm SL. The smallest (<20 mm SL) were present both years into mid-September, after which no new settlers were detected (Fig. 5). Significantly higher mean SLs were detected by late August in both years compared with earlier sample periods; size significantly increased with season (ANOVA, $P \leq 0.05$; Table 2; Fig. 5). Fish were significantly larger earlier in 1995, but fish from 1994 caught up in size by September, after which 1994 fish were significantly larger than 1995 fish (ANOVA, $P \leq 0.05$; Table 2; Fig. 5).

In 1994, age-0 red snapper were first abundant (CPUE=63.6) at station 1 and had limited settlement (CPUE=2.0) at station 3 (Fig. 6). Also, fish were significantly larger (ANOVA, $P \leq 0.05$), less abundant, and showed up later at all other stations compared with fish at station 1 in 1994. We did not detect patterns in inshore-offshore movement from fish size, location, and seasonality; we did determine that after first settlement at station 1, fish showed expansion in all directions (Fig. 6). In 1995, new recruits were most abundant in July at station 3 (CPUE=78). After July, patterns were similar to 1994, and most fish were observed at station 1 and fewer larger fish were observed at other stations later in the season (Fig. 7).

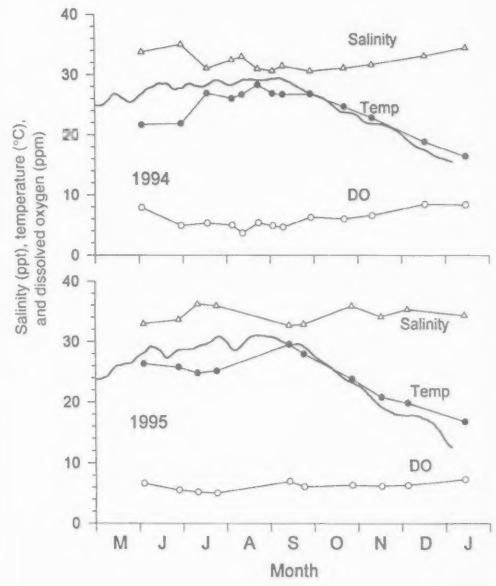


Figure 2

Bottom water temperature (°C), salinity (ppt), and dissolved oxygen (ppm) pooled by stations, in the northeast Gulf of Mexico, from June 1994 to January 1995, and June 1995 to January 1996. Lines without symbols are mean daily surface temperatures based on 10-d moving averages, obtained from a NOAA moored buoy.

The required precision (≤10%), was shown for 57% of all otolith counts (Table 3). Age of red snapper was 26 to 144 days; thus fish may spend up to four months in these habitats. We detected separate late May–June and July cohorts in 1994, and May and June cohorts in 1995, from hatching-date frequencies (Fig. 8).

Growth rates were significantly different among cohorts (ANCOVA, $P \leq 0.05$). The fastest growth rates were observed for June (0.77 mm/d) and July (0.71 mm/d) cohorts in 1994. Growth rates for May (0.51 mm/d) and June (0.67 mm/d) cohorts in 1995 were significantly less than the previous year and significantly different from each other (ANCOVA, $P \leq 0.05$; Fig. 9). Growth rate estimates from SL on varying dates (0.52 mm/d in 1994; 0.62 mm/d in 1995; Fig. 5) were significantly lower than most cohort growth estimates, with the exception of the slow growing May 1995 cohort (ANCOVA, $P \leq 0.05$). In station comparisons for 1995, fish from station 2 had a significantly faster growth rate (0.86 mm/d), followed by fish from station 1 (0.71 mm/d), whereas slower growth rates were observed for station 3 (0.54 mm/d) and station 5 (0.60 mm/d; ANCOVA, $P \leq 0.05$; Table

Table 1

Mean temperatures, mean salinities, mean dissolved oxygen (DO), depths, and +SEs substrate types for trawl stations from the northeast Gulf of Mexico. See Figure 1, for station locations.

Station	Mean temperature (°C)	Mean salinity (ppt)	Mean DO (ppm)	Depth (m)	Substrate type
1994					
1	24.5+1.0	32.7+0.5	5.4+0.4	18.7+0.6	fine sand-shell
2	24.6+1.3	29.9+0.9	6.1+0.5	15.6+0.6	coarse sand
3	24.3+1.4	31.7+0.7	6.1+0.5	13.4+0.6	silt, clay, sand
4	24.9+1.3	32.3+0.5	6.3+0.4	15.0+0.4	coarse sand
5	24.6+1.2	32.7+0.5	6.3+0.4	20.7+0.6	fine sand
1995					
1	24.0+1.2	35.5+0.7	6.3+0.4	19.5+0.1	fine sand-shell
2	25.3+1.2	32.6+0.4	6.2+0.2	16.1+0.7	coarse sand
3	22.6+1.3	33.6+1.3	5.5+0.5	12.7+0.2	silt, clay, sand
4	23.6+1.2	35.6+0.4	6.1+0.2	14.8+0.2	coarse sand
5	23.8+1.3	34.8+0.9	6.5+0.3	20.8+0.2	fine sand

4). Station 4 growth rates were not estimated because of low catch rates.

Discussion

Age-0 red snapper used inner shelf habitat at first settlement, and an area 13 km south of Mobile Bay (station 1) held particularly high numbers. No other study has reported such high CPUEs of age-0 red snapper. Many factors could contribute to this important nursery habitat at station 1. Temperature, dissolved oxygen, salinity, and depths, showed little difference among stations, but one potential aspect that may provide avenues for future studies is substrate type. The substrate in this area may be highly suitable, e.g. relic shell beds (Schroeder et al., 1995) with fine sand sediments, and there is a general shift from shell-sand-mud to "clean" sand east of Mobile Bay,[1] where few fish were collected. Age-0 red snapper may be selecting such shell habitats. For example, age-0 red snapper showed a preference for shell over sand substrata in laboratory studies (Szedlmayer and Howe, 1997)and a preference for almost any small relief structure (e.g. shells) in relation to flat sand substrata in natural habitats (Workman and Foster, 1994). Shells were observed in trawl collections at station 1 and not apparent in trawl samples at other stations. However, we were un-

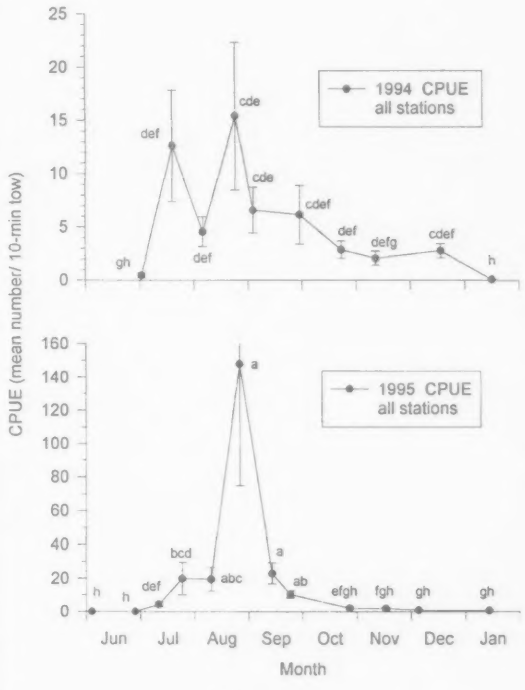


Figure 3

Mean CPUE (number/10-min tow) of age-0 red snapper, *Lutjanus campechanus*, by date from the northeast Gulf of Mexico. Each point represents mean CPUE for that date. Error bars are standard errors. Different letters show significant differences both within and between years (ANOVA; Waller-Duncan test; $P \leq 0.05$).

[1] Hummell, R. L. 1998. Geological survey of Alabama, Tuscaloosa, AL. Personal commun.

able to confirm the presence of shell deposits from sediments collected by SCUBA divers.

Red snapper first settled in June, showed peaks in July, August, and September, then quickly declined in numbers from the habitat. There is evidence that this decline of age-0 red snapper from open relatively flat habitats in the fall results from larger age-0 fish migrating to reef structure. In a study of fish recruitment to 1-m^3 concrete artificial reefs, 20 km south of Mobile Bay, age-0 red snapper showed large (up to 89 fish/reef) influxes to these reefs in September and October.[2] This seasonal pattern was similar to the pattern suggested by Holt and Arnold (1982). They found that recruitment of small red snapper to benthic substrate occurred primarily from June through September, and in the fall a few larger age-0 fish were collected by trap near a sunken ship.[3]

Metamorphosis from larva to juvenile is ecologically important in the early life history of fish. In

Table 2

Mean SL (mm) of age-0 red snapper, *Lutjanus campechanus*, for each sample date in 1994 and 1995, from the northeast Gulf of Mexico. Means with different letters show significant differences (ANOVA, Waller-Duncan's test; $P<0.05$).

Date	*n*	Mean SL (mm)	SE
30 June 94	5	25.0[a]	2.01
11 July 94	328	24.1[a]	0.19
1 August 94	121	36.1[e]	0.64
11 August 94	137	26.6[a]	0.72
17 August 94	401	36.1[e]	0.66
30 August 94	165	41.6[d]	1.22
8 September 94	322	42.9[d]	0.46
26 September 94	154	70.5[hg]	1.88
13 October 94	72	75.4[i]	1.59
31 October 94	54	85.9[j]	1.28
14 December 94	42	99.2[k]	3.12
10 January 94	2	116.1[l]	8.35
11 July 95	108	33.2[bc]	0.62
24 July 95	454	31.8[b]	0.40
9 August 95	485	35.5[bc]	0.35
25 August 95	3696	41.1[d]	0.08
12 September 95	572	57.1[e]	0.38
22 September 95	259	66.5[fg]	0.66
25 October 95	53	60.8[e]	2.36
14 November 95	44	72.7[hi]	2.52
2 December 95	18	65.3[f]	4.83
10 January 96	15	89.4[j]	4.67

Table 3

Comparison of otoliths prepared and percent accepted for estimation of age in age-0 red snapper, *Lutjanus campechanus*.

Date	Otoliths prepared	Otoliths with >10% precision	Percent accepted
11 Jul 94	318	172	54
17 Aug 94	316	149	47
8 Sep 94	322	118	37
10–13 Jul 95	108	78	72
9–10 Aug 95	245	180	73
11–13 Sep 95	279	160	57
Total	1588	857	57

[2] Szedlmayer, S. T. 1994. Production or attraction: an evaluation of artificial reefs in coastal Alabama. Alabama Universities Tennessee Valley Research Consortium Final Report, Auburn University, Auburn, AL, 48 p.

[3] Holt, S. A. 1997. Marine Science Institute, Univ. Texas, Port Aransas, TX. Personal commun.

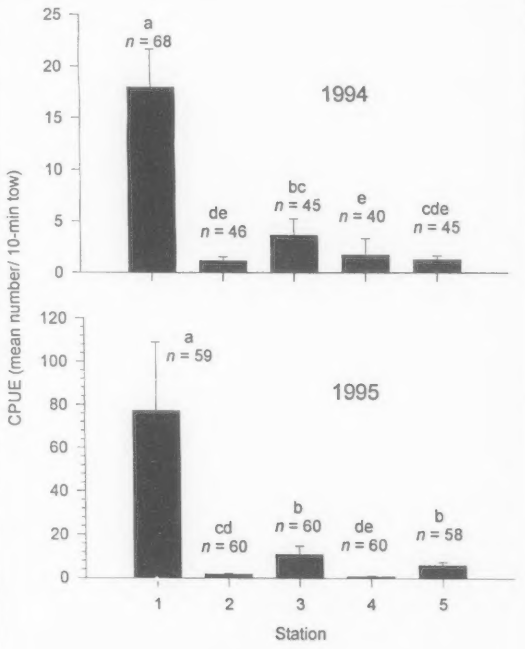


Figure 4

Mean CPUE (number/10-min tow) of age-0 red snapper, *Lutjanus campechanus*, by station from the northeast Gulf of Mexico. Error bars are standard errors, and *n*'s are number of trawl tows. Different letters show significant differences both within and between years (ANOVA; Waller-Duncan test; $P\leq0.05$).

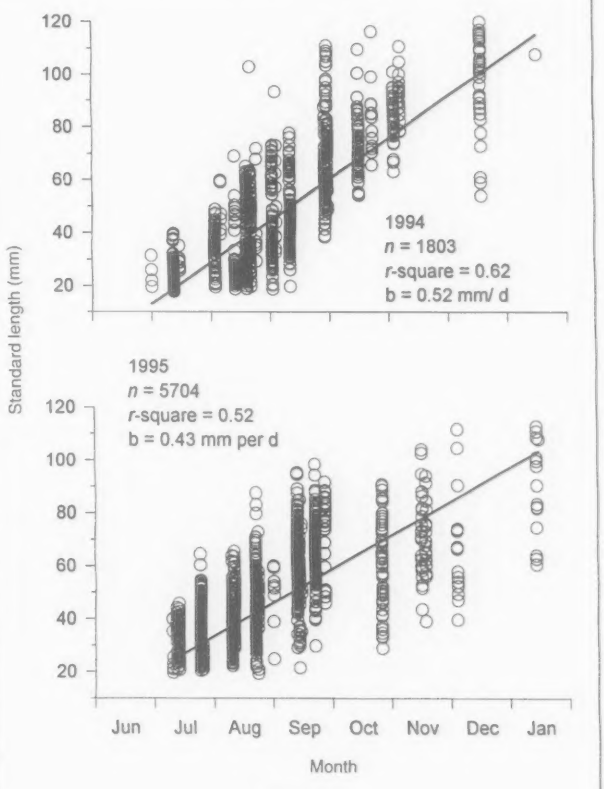


Figure 5

Linear regression of age-0 red snapper, *Lutjanus campechanus*, SL on date for 1994 and 1995, for all fish collected from the northeast Gulf of Mexico. Data points are individual fish. Growth rates were significantly different between years (t-test; $P \leq 0.05$).

many fish species this transition occurs simultaneously with habitat change, i.e. from pelagic larvae to benthic juveniles. On the basis of smallest fish collected during this study, larval red snapper metamorphose near 26 d and at 18 mm in length. Collins et al. (1980) suggested similar settlement sizes (12.4 to 22.4 mm SL) from plankton net samples.

Age-0 red snapper otoliths had daily microincrements when growth rates were >0.3 mm/d (Szedlmayer, 1998). In the present study, the nursery period was in the warmer summer months, when food should be abundant; and by all indications, growth rate far exceeded the 0.3 mm/d threshold rate. Thus, back calculation of first increment formation accurately estimated hatching date for age-0 red snapper. One difficulty with the otolith ageing methods was the low (57%) percentage of otoliths that met the required predetermined precision. However, this low percentage was due to personnel skill in otolith preparation. For example, an inexperienced technician would typically over polish several otoliths, that were subsequently rejected when counting. This same technician, after gaining experience and in-

Table 4

Comparison of growth rates among selected stations in 1995. Means with different letters show significant differences (ANCOVA, Tukey's test; $P \leq 0.05$).

Station	Growth rate mm/d	n	r^2
1	0.71[a]	227	0.86
2	0.86[b]	25	0.89
3	0.54[c]	115	0.80
5	0.60[c]	49	0.76

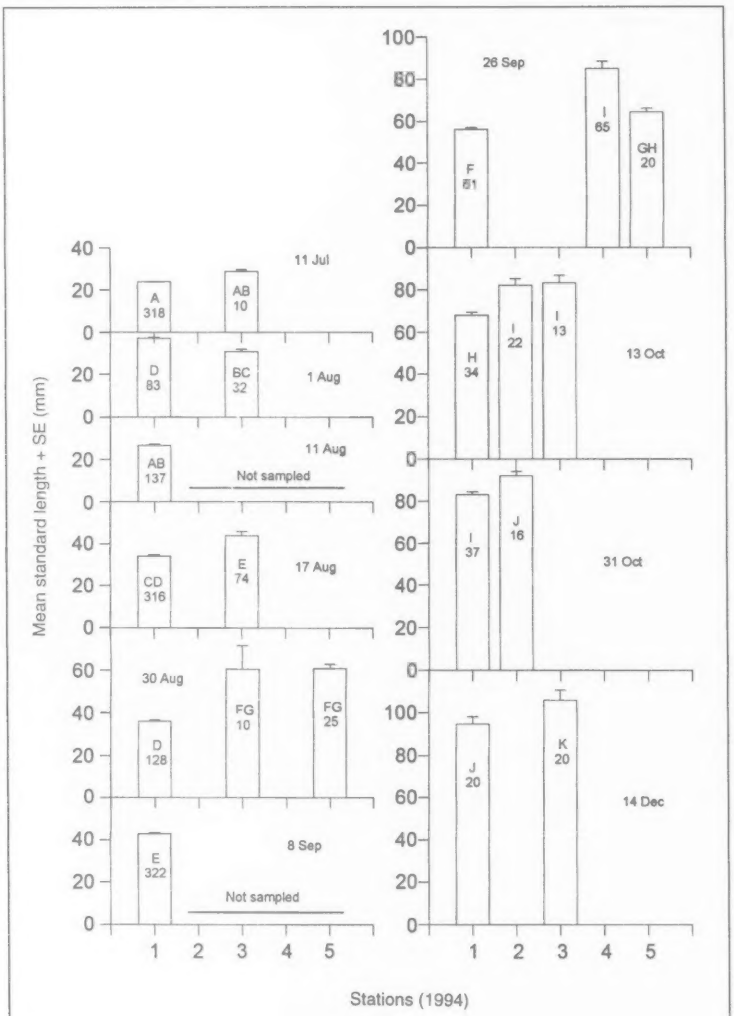


Figure 6

Mean standard lengths by station and date in 1994 for all collections that had ≥10 fish. Numbers in bars are number of fish measured. Different letters show significant differences among stations and dates (ANOVA; Waller-Duncan test; $P \leq 0.05$).

creased skill, would make an acceptable preparation of the second otolith from the same fish.

Hatching-date distributions clearly indicated separate hatching cohorts with peaks approximately one month apart. The multiple spawnings within a given year in red snapper may be an adaptation to increase survival. By spreading reproductive efforts over time, a species may increase the probability of matching the correct biotic and abiotic conditions for enhanced survival and subsequent recruitment.

Two differences were apparent when hatching-date estimates were compared with estimated spawning periods from gonadosomatic index (GSI) maxima (Collins et al., 1996). First, GSI estimates showed little indication of May spawning, as suggested by May hatching dates in the present study; and second, present estimates showed little indication of August spawning, as indicated by high GSIs for red snapper in August (Collins et al. 1996). These differences between hatch dates and GSIs were probably

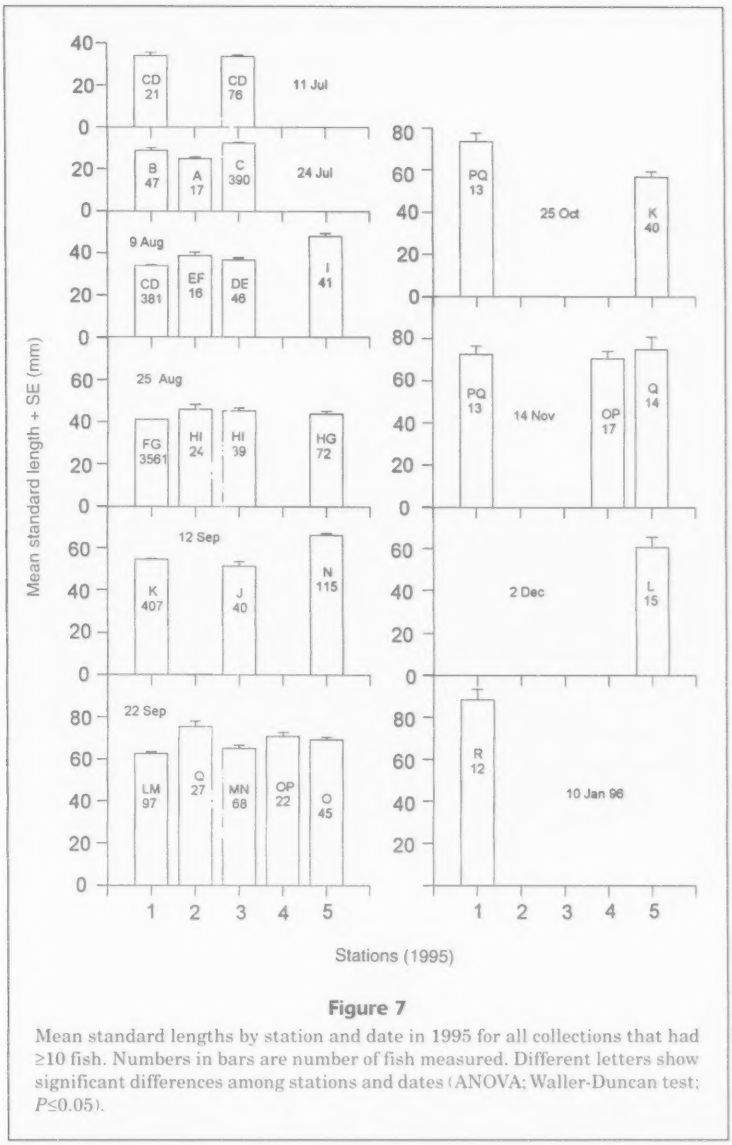


Figure 7

Mean standard lengths by station and date in 1995 for all collections that had ≥10 fish. Numbers in bars are number of fish measured. Different letters show significant differences among stations and dates (ANOVA; Waller-Duncan test; $P \leq 0.05$).

due to yearly variation. Collins et al. (1996) sampled from 1991 to 1993. Lack of evidence for August spawning in our study may also have resulted from low survival of later spawned fish or from new recruits having settled to different habitats not sampled in the present study.

The June and July 1994 cohorts had growth rates that were significantly faster in relation to 1995 cohort growth rates. Growth rates estimated from SL on varying dates were probably inaccurate owing to extended settlement of new recruits, but results showed the same pattern as SL on age estimates, i.e. 1994 growth rates were significantly faster compared with 1995 estimates (t-test, $P \leq 0.05$; Fig. 5). If growth rates were an indication of the probability of survival (Houde, 1989; Sogard, 1997), then 1994 cohorts may have had an advantage over the 1995 spawned cohorts. Growth rate typically decreases with decreasing temperature and may have resulted in the low growth rate observed for the May 1995 cohort. Thus, it appears that both density dependent and density independent mechanisms are operating

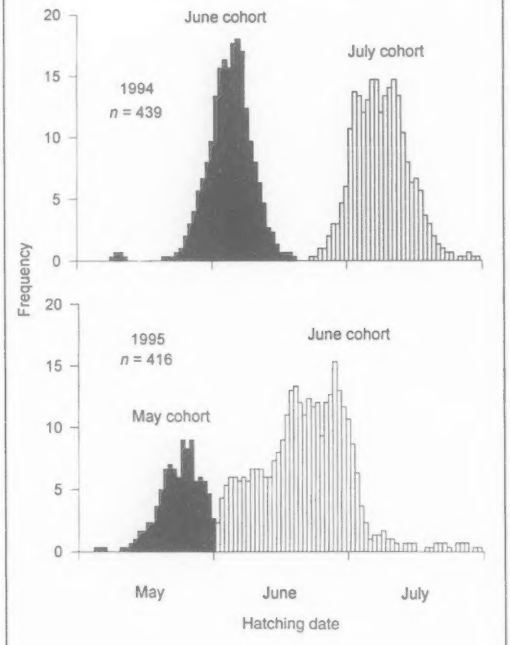


Figure 8

Hatch date frequencies of age-0 red snapper, *Lutjanus campechanus*, pooled over all dates from 1994 and 1995. A three day moving average was applied before plotting.

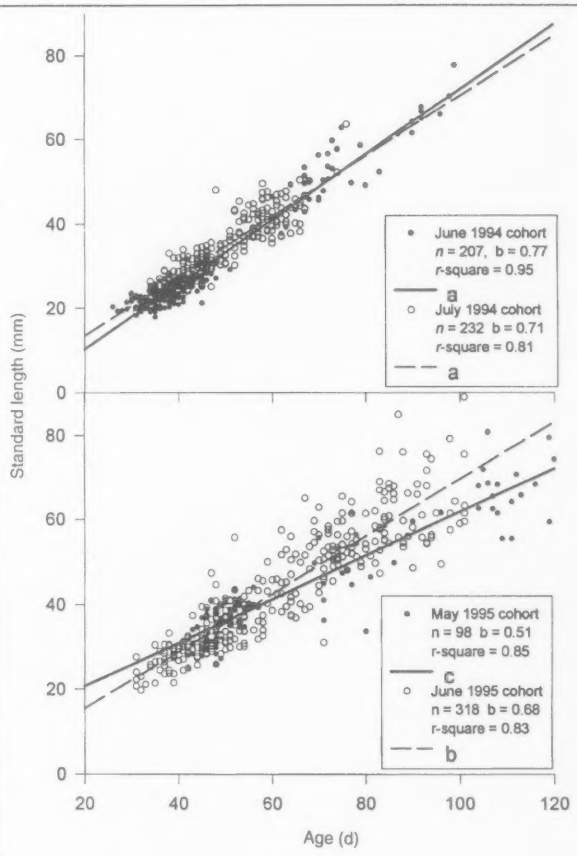


Figure 9

Growth rates of separate cohorts of age-0 red snapper, *Lutjanus campechanus*, from SL on age regressions from the northeast Gulf of Mexico. Data points are individual fish. Different letters show significant differences among cohorts both within and between years (ANCOVA; Tukey's test; $P \leq 0.05$).

(Bromley, 1989; Rijnsdorp and Vanleeuwen, 1992; Rogers, 1994). In 1994, there were fewer fish but faster growth rates than those in 1995, and in 1995 the early May cohort showed the slowest growth rates, probably from colder temperatures. This scenario suggests that if red snapper spawn early (May), temperature may play an important role. As the season progresses into July and August, temperature increases, settlement increases, and competition for food and shelter may become the limiting factors, such that later spawnings in August have lower survival.

The inner shelf habitat in the northeast Gulf of Mexico, particularly the location 13 km south of Mobile Bay, Alabama, should be considered an important nursery area for age-0 red snapper from July through September. Future research should address mechanisms that help to define this red snapper nursery habitat, and back calculation methods could be used to compare the relative contributions of various within-year cohorts to subsequent year classes.

Acknowledgments

We thank Jason Lee for help in field collections and otolith preparation. We also thank Karen Belcolore for data entry and for typing the manuscript. This study was funded by NOAA, NMFS, MARFIN grant number USDC-NA47FF0018-0.

Literature cited

Baughman, J. L.
1943. The lutjanid fishes of Texas. Copeia 43:212–15.

Bradley, E., and C. E. Bryan.
1975. Life history and fishery of the red snapper (*Lutjanus campechanus)* in the northwestern Gulf of Mexico: 1970–1974. Proc. 27th Annu. Gulf Caribb. Fish. Inst. and 17th Annu. Int. Game Fish Res. Conf. 27:77–106.

Bromley, P. J.
1989. Evidence for density-dependent growth in North Sea gadoids. J. Fish Biol. 35:117–123.

Collins, L. A., J. H. Finucane, and L. E. Barger.
1980. Description of larval and juvenile red snapper, *Lutjanus campechanus*. Fish. Bull. 77:965–974.

Collins, L. A., A. G. Johnson, and C. P. Keim.
1996. Spawning and annual fecundity of the red snapper (*Lutjanus campechanus*) from the northeastern Gulf of Mexico. *In* F. Arreguin-Sanchez, J. L. Munro, M. C. Balgos, and D. Pauly (eds.), Biology, fisheries and culture of tropical groupers and snappers, p. 174–188. ICLARM Conf. Proc. 48, Makati City, Philippines.

Holme, N. A., and A. D. McIntyre.
1971. Methods for the study of marine benthos. IBP handbook no. 16. Blackwell Scientific Publications, Oxford, 334 p.

Holt, S. A., and C. R. Arnold.
1982. Growth of juvenile red snapper *Lutjanus campechanus*, in the northwestern Gulf of Mexico. Fish. Bull. 80:644–648.

Houde E. D.
1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Sym. 2:17–29.
1989. Subtleties and episodes in the early life of fishes. J. Fish Biol. 35:29–38.

Lambert, T. C., and D. M. Ware.
1984. Reproductive strategies of demersal and pelagic spawning fish. Can. J. Fish. Aquat. Sci. 41:1565–1569.

Miranda, L. E., and W. D. Hubbard.
1994. Length-dependent winter survival and lipid composition of age-0 largemouth bass in Bay Springs Reservoir, Mississippi. Trans. Am. Fish. Soc. 123:80–87.

Moseley, F. N.
1966. Biology of the red snapper, *Lutjanus aya* Bloch, of the northwestern Gulf of Mexico. Publ. Inst. Mar. Sci. Univ. Texas 11:90–101.

Ogren, L. H., and H. A. Brusher.
1977. The distribution and abundance of fishes caught with a trawl in the St. Andrew Bay system, Florida. Northeast Gulf Science 1(2):83–105.

Rijnsdorp, A. D., and P. I. Vanleeuwen.
1992. Density-dependent and independent changes in somatic growth of female North Sea plaice, *Pleuronectes platessa*, between 1930 and 1985 as revealed by back-calculation of otoliths. Mar. Ecol. Prog. Ser. 88:19–32.

Rogers, S. I.
1994. Population density and growth rate of juvenile sole *Solea solea* (L.). Neth. J. Sea Res. 32:353–360.

Schroeder, W. W., A. W. Shultz, and O. H. Pilkey.
1995. Late quaternary oyster shells and sea-level history, inner shelf, northeast Gulf of Mexico. J. Coast. Res. 11:664–674.

Secor, D. H., J. M. Dean, and E. H. Laban.
1991. Manual for otolith removal and preparation for microstructural examination. Electric Power Res. Inst. and Belle W. Baruch Inst. Mar. Biol. Coast. Res., Columbia, SC, 85 p.

Sogard, S. M.
1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. 60:1129–1157.

Spurr, A. R.
1969. A low-viscosity epoxy resin embedding medium for electron microscopy. J. Ultrastruct. Res. 26:31–43.

Szedlmayer, S. T.
1998. Comparison of growth rate and formation of otolith increments in age-0 red snapper. J. Fish Biol. 52:58–65.

Szedlmayer, S. T., and J. C. Howe.
1997. Substrate preference in age-0 red snapper, *Lutjanus campechanus*. Environ. Biol. Fish. 50:203–207.

Szedlmayer, S. T., and R. L. Shipp.
1994. Movement and growth of red snapper, *Lutjanus campechanus*, from an artificial reef area in the northeastern Gulf of Mexico. Bull. Mar. Sci. 55:887–896.

Szedlmayer, S. T., M. M. Szedlmayer, and M. E. Sieracki.
1991. Automated enumeration by computer digitization of age-0 weakfish *Cynoscion regalis* scale circuli. Fish. Bull. 89:337–340.

Szedlmayer, S. T., M. P. Weinstein, and J. A. Musick.
1990. Differential growth among cohorts of age-0 weakfish *Cynoscion regalis* in Chesapeake Bay. Fish. Bull. 88:745–752.

Workman, I. K., and D. G. Foster.
1994. Occurrence and behavior of juvenile red snapper, *Lutjanus campechanus*, on commercial shrimp fishing grounds in the northeastern Gulf of Mexico. Mar. Fish. Rev. 56:9–11.

Zar, J. H.
1984. Biostatistical analysis, 2nd edition. Prentice Hall, Inc., Englewood Cliffs, NJ, 718 p.

Abstract.—This study examined the relation between statolith and somatic growth in the tropical squid *Sepioteuthis lessoniana*. Five separate linear dimensions were measured on the statoliths of 103 individuals (17–245 mm mantle length). In addition the statoliths of 80 adults (82–245 mm mantle length) were weighed. Statolith increment analysis provided age estimates for 78 individuals. Statolith total length was correlated with age for squid less than ~60 days of age, although neither statolith total length nor weight was a useful predictor of age in older squid. Combining the five statolith dimensions to produce a description of statolith shape provided only slightly better estimates of age than statolith total length or weight alone. Statolith shape changed during ontogeny, developing from relatively elongate juvenile statoliths into the adult form with more robust dorsal and lateral domes. This development was reflected in wider spacing and superior optical definition of daily growth increments in the dorsal and lateral domes of adult statoliths, in relation to the slower growing rostrum. Growth of *S. lessoniana* statoliths does not appear to be strongly linked to mantle growth; both statolith total length and weight increase more slowly than mantle length.

Manuscript accepted 12 August 1998.
Fish. Bull. 97:636–645 (1999).

Ontogenetic changes in size and shape of statoliths: implications for age and growth of the short-lived tropical squid *Sepioteuthis lessoniana* (Cephalopoda: Loliginidae)

Ross Thomas

Natalie A. Moltschaniwskyj

School of Marine Biology and Aquaculture
James Cook University
Townsville, Queensland 4811, Australia.
Present address (for N. A. Moltschaniwskyj, contact author): School of Aquaculture
University of Tasmania
PO Box 1214
Launceston, Tasmania 7250, Australia.

E-mail (for N. A. Moltschaniwskyj, contact author): natalie.moltschaniwskyj@utas.edu.au

Knowledge of the age structure and growth rates in naturally occurring populations is fundamental to estimating demographic parameters and evaluating ecological processes. Periodic growth increments in squid statoliths are a reliable and accurate tool for determining the age structure of squid populations (Villanueva, 1992; Arkhipkin, 1993; Bigelow, 1994; Jackson, 1994). Growth-rate calculations based on statolith age estimates indicate that tropical squid are short-lived and grow continuously throughout their lifespan (Jackson, 1990; Jackson and Choat, 1992). Growth rates of tropical squid can be strongly influenced by changes in their environment, including temperature fluctuations (Forsythe and Hanlon, 1989), and availability of food (Forsythe, 1993). Consequently, growth rates, final size, and response to changing conditions of tropical squid may vary greatly within or between species (Jackson, 1990; Jackson and Choat, 1992). Apart from obtaining size-at-age information from statoliths, there is also the potential to obtain ecological information on past growth histories of some squid species (Jackson, 1994). Any attempts made at constructing growth histories of squid based on statolith microstructure will benefit greatly from a thorough understanding of growth and development of the statolith and how this relates to growth of somatic tissue.

Daily growth increments in fish otoliths, which are analogous to those in squid statoliths (Radtke, 1983), provide valuable data on the age structure and growth rates of exploited fish species (Campana and Neilson, 1985; Jones, 1986; Stevenson and Campana, 1992). Recent studies of fish somatic-otolith growth relationships may contribute to investigations of somatic-statolith growth relationships in squid. Evidence exists supporting the direct relationship between age and otolith weight for several fish species (Boehlert, 1985; Fletcher, 1991), although further validation is required before otolith weight can be used reliably to estimate age. Several authors have also demonstrated that slower-growing fish have larger otoliths than similar sized, faster-growing individuals (Mosegaard et al., 1988; Secor and Dean, 1989; Wright et al., 1990;

Mugiya and Tanaka, 1992), indicating a possible disassociation between otolith and somatic growth. Similarly, disassociation between statolith and somatic tissue growth has been demonstrated in the tropical loliginid squid *Loligo chinensis* (Jackson, 1995), and also in two ommastrephid squids, *Todarodes angolensis* and *Todaropsis eblanae* (Lipinski et al., 1993).

The periodic growth increments in squid statoliths are bipartite structures consisting of a discontinuous zone and an incremental zone comprising aragonite ($CaCO_3$) crystals (Lipinski, 1986). Specific morphological differences in the aragonite crystal structure have been illustrated between statolith regions within several squid species (Lipinski, 1993). Crystals of the lateral dome region often display greater variation in shape, size, and orientation than the more homogenous wing crystals (Lipinski, 1993). These variations in crystal structure suggest that accretion is not uniform and that different regions of the statolith may grow at different rates.

The present study provides an assessment of the growth and shape of *Sepioteuthis lessoniana* statoliths based on the linear measurement of statolith dimensions. The potential for using statolith shape descriptions as a proxy for age estimations and the relation between statolith and somatic tissue growth in these squid are examined. Overall descriptions of individual statolith shape covered a broad length and weight range of squid, providing a basis for comparison with age estimates determined by using traditional analysis techniques. With the increased use of statoliths in squid age and growth studies, it is important to understand how statoliths grow and how this growth relates to growth of somatic tissue.

Materials and methods

Study species and collection methods

A total of 103 *Sepioteuthis lessoniana* individuals were captured from waters around the Townsville region of north Queensland, Australia, between January and August 1995. Twenty-three juvenile squid (16–43 mm mantle length [ML]) were captured by using purse seines and dip nets. Juveniles often shelter in surface waters among floating debris or artificially constructed shade devices and are easily netted. Eighty adult squid (82–245 mm ML) were captured from coastal waters at night with squid jigs and by means of light attraction. Individuals were separated into two age groups for these descriptions: juvenile (≤60 days) and adult (>60 days). This separation was based on the techniques used to capture the individuals, which may be related to differences in life style and ecology.

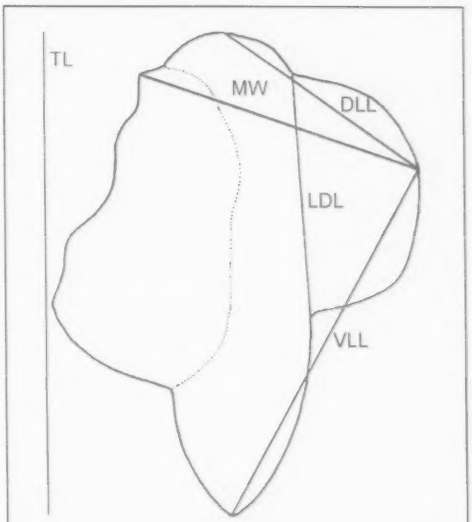


Figure 1

Sepioteuthis lessoniana statolith showing the dimensions measured for morphometric analyses. TL = total statolith length; DLL = dorsolateral length; VLL = ventrolateral length; LDL = lateral dome length; MW = maximum width.

Size measurements

Mantle length was measured from all *Sepioteuthis lessoniana* specimens upon capture. Wet weight was not obtained for the majority of individuals because of the inability to weigh animals accurately on a boat. Statoliths were removed and stored in 70% alcohol, and adult statoliths were later weighed to the nearest 0.01 mg. Weights of juvenile statoliths were not recorded because they were too small to obtain accurate measurements. Five dimensions were measured from each statolith following the descriptions of statolith shape by Clarke (1978): total length, dorsolateral length, ventrolateral length, lateral dome length, and maximum width (Fig. 1). Dimensions were measured from whole statoliths viewed with the anterior (concave) side positioned upward by using an Ikegami-290 high-resolution black and white video camera mounted on a compound microscope. Squid ages were estimated by using statolith increment analysis on ground and polished statoliths (Jackson, 1990). All increment counts were made in the dorsal-dome region of statoliths because increment definition was consistently clearest in this area. Age estimates for 62

adult and 16 juvenile squid were calculated from a mean of three separate counts made by one reader.

Statistical analyses

Paired-sample t-tests indicated no significant difference between left and right statolith total length measures (t=0.67, df=101, P=0.50, n=102), or adult statolith weight measures (t=0.47, df=79, P=0.64, n=80), but wherever possible, the left statolith was used for analyses. For the purpose of this study, statolith "size" refers to the length of each statolith dimension, whereas "shape" indicates that all statolith dimensions have been combined to describe overall statolith structure.

Rates of growth calculated from size-at-age data were not significantly different between adult males and females (Table 1). A size comparison of males and females, adjusted for age, found no significant difference in size between the sexes (Table 2). Individuals were therefore classified as either juveniles or adults, with no distinction made between adult sexes. This classification avoided over-complicating analyses and also provided a larger adult sample size.

Principal components analysis (PCA) was performed on statolith dimensions with the covariance matrix of transformed ($\log_{10}$) data, allowing complete descriptions of statolith shape for all dimensions simultaneously. The magnitude of coefficients in the first eigenvector varies because of changing statolith proportions and relative growth patterns. These coefficients indicate the nature of allometric growth for each variable (dimension) (Jolicoeur, 1963). The coefficients for each variable in the first eigenvector describe the relative growth rates of all the components simultaneously (Shea, 1985). Variables with coefficient scores on the first principal component vector equal to the mean coefficient ($(1/p)^{0.5}$, where p is the number of variables in the analysis) are isometric. Positive and negative allometry is indicated by values greater than and less than the mean coefficient, respectively (Jolicoeur, 1963).

The resampling technique jack-knifing provided means and standard errors (SE) of each coefficient (Marcus, 1990). The probability that the mean coefficient was significantly different from the hypothesized value (Marcus, 1990) is

$$P\left(\begin{array}{c}|mean\ coefficient - hypothesized\ coefficient| \\ > T \times SE \times mean\ coefficient\end{array}\right) < 1/T^2 \quad (1)$$

where T = the number of standard errors for which the probability statement is made.

In this case T = 4.47 provides a probability of 0.05. Simply, the difference between the mean coefficient and the hypothesized coefficient is greater than a critical difference ($T \times$ SE $\times$ calculated coefficient) with a probability $<1/T^2$.

Table 1

Linear regression equations for the size-at-age data of male and female *Sepioteuthis lessoniana*. SE_b = standard error of the slope. *ML*=mantle length (mm). H_o for t-test: $b = 0$.

Sex	n	Equation	SE_b	r^2	t	P
Male	32	$age = 0.08ML + 5.02$	0.02	0.44	4.84	0.0001
Female	31	$age = 0.08ML + 5.44$	0.02	0.43	4.64	0.0001

Results

Statolith size relationships

The smallest statolith total length (648 μm) was observed in the youngest specimen (17 days old). The largest adult statolith total length (2167 μm) was observed in a 162-day-old mature female, although

Table 2

Analysis of covariance table, comparing mantle length (ML) of male and female *Sepioteuthis lessoniana*, using age as a covariate.

Source	df	Sum of squares	Mean square	F-value	$P > F$
Test for equal slopes					
Sex	1	1.46	1.46	0.32	0.5764
Age (covariate)	1	329.60	329.60	71.21	0.0001
Sex × age (equal slopes)	1	1.20	1.20	0.26	0.6128
Test for differences in ML					
Sex	1	0.40	0.40	0.09	0.7681
Age (covariate)	1	333.23	333.23	73.01	0.0001

the oldest individual was a 186-day-old mature female. Adult statolith weights ranged from 0.29 mg in a 72-day-old immature male to 1.74 mg in a 144-day-old mature female.

Adult statolith weight was not a reliable predictor of squid age, with only 57% (n=62) of the variation in adult ages attributable to weight of the statoliths (Fig. 2A). The strength of the relation between age and statolith total length differed between juvenile and adult squid (Fig. 2B). For juvenile squid, 85% (n=16) of the variation in age was attributable to differences in statolith total length, indicating statolith total length maintains a close correlation with age during the first 60 days of squid growth. In adult squid, the ability to predict age based on statolith total length is poor, and only 57% (n=62) of the variation in squid ages can be explained by statolith length. Statolith total length grew relatively slower than ML for both adult and juvenile squid (Fig. 3A). Adult statolith weight displayed positive allometric growth with ML (Fig. 3B).

Changes in statolith shape

The first PCA axis described 98.6% of the variation among individuals, which is due to statolith shape or the size of all statolith dimensions combined. If we use the PCA score on the first axis as a descriptor of statolith shape, we can account for only 9% and 7% of the variation in statolith total length of juvenile (n=16) and adult (n=78) squid, respectively (Fig. 4B). This result confirms that the first PCA axis contains statolith shape information and not predominantly size information. Growth of the statolith along the total length, ventrolateral and lateral dome axes and in total length was relatively slow, as evidenced by negative allometric growth (Table 3). In contrast, growth of the statolith along the dorsolateral axis and in total width grew relatively faster, as evidenced by the positive allometric growth (Table 3). This finding indicates that the statoliths of juvenile squid are relatively thin and elongate, becoming comparatively

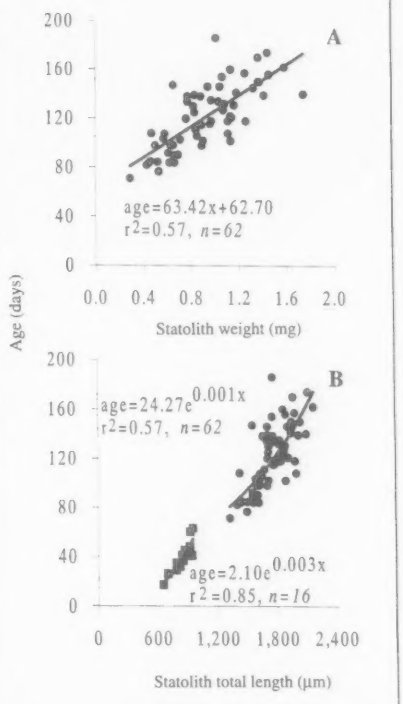


Figure 2

Relationship between (**A**) adult statolith weight and age, and (**B**) statolith total length and age for *Sepioteuthis lessoniana* specimens. Circles = adults; squares = juveniles.

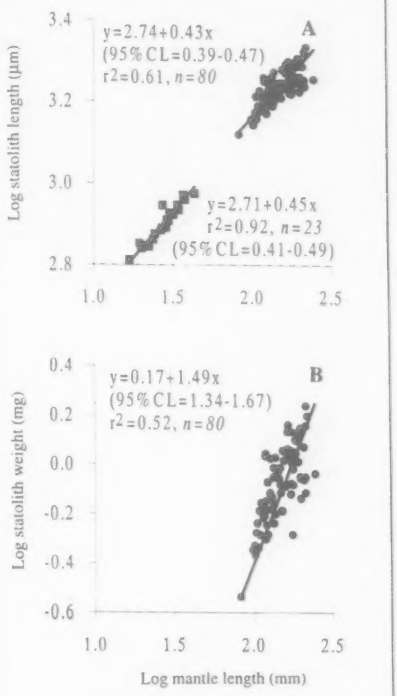


Figure 3

Relation between (**A**) mantle length and statolith total length, and (**B**) mantle length and adult statolith weight for *Sepioteuthis lessoniana* specimens. Circles = adults; squares = juveniles. CL = confidence limits of the slope.

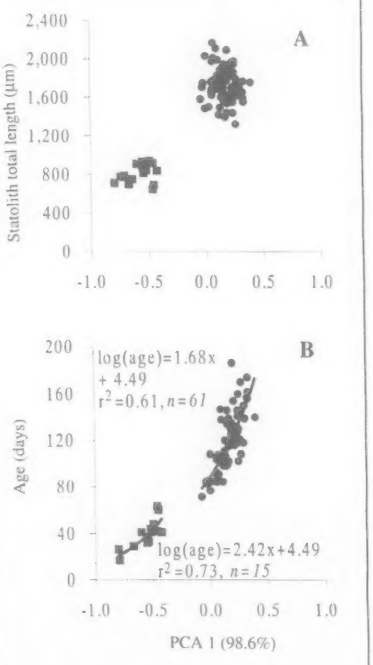


Figure 4

Relative growth of the length of statolith dimensions. The relation between the principal component score on the first axis for each statolith against (**A**) statolith total length, and (**B**) age. The percentages indicate the variation in the data set that has been described by each principal component axis. Circles = adults; squares = juveniles.

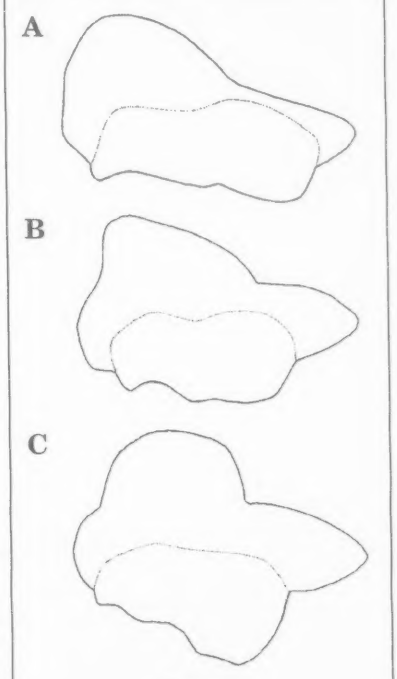


Figure 5

Statoliths of *Sepioteuthis lessoniana*, demonstrating the change in shape from juvenile to adult squid. Mantle lengths and total statolith lengths were (**A**) 16 mm, 648 µm; (**B**) 119 mm, 1525 µm; (**C**) 190 mm, 1875 µm, respectively. Statoliths are shown in anterior view at different scales to facilitate shape comparison.

Table 3

Relative growth of statolith dimensions. Coefficient = coefficient of the first eigenvector. Isometric growth occurs when the coefficient equals $(1/p)^{0.5} = 0.447$. The difference equals the coefficient minus 0.447, which must be greater than the critical difference if allometric growth has occurred; data are $\log_{10}$-transformed; SE = standard errors.

	Coefficient				
Variable	Mean	SE	Critical difference	Difference	Allometric growth
Total length	0.435	0.004	± 0.008	–0.012	negative
Dorsolateral	0.503	0.010	± 0.022	0.056	positive
Ventrolateral	0.387	0.006	± 0.010	–0.060	negative
Lateral dome	0.349	0.005	± 0.008	–0.098	negative
Total width	0.535	0.007	± 0.017	0.088	positive

fatter and bulkier during growth (Fig. 5). Statoliths of the adults continued to grow (Fig. 3); however, there is no relation between the PCA score on the first axis and statolith size for the adults (Fig. 4A), suggesting that the overall shape of individual adult statoliths showed no further change.

Table 4

Relative growth of statolith dimensions. The coefficients for the first three principal component axes (PCA) of the analysis on length variables; data are $\log_{10}$-transformed and the covariance matrix was used.

	Eigenvector		
Variable	PCA 1	PCA 2	PCA 3
Total length	0.435	0.308	0.154
Dorsolateral	0.503	–0.695	0.321
Ventrolateral	0.387	0.592	–0.108
Lateral dome	0.349	0.210	0.579
Total width	0.535	–0.163	–0.726

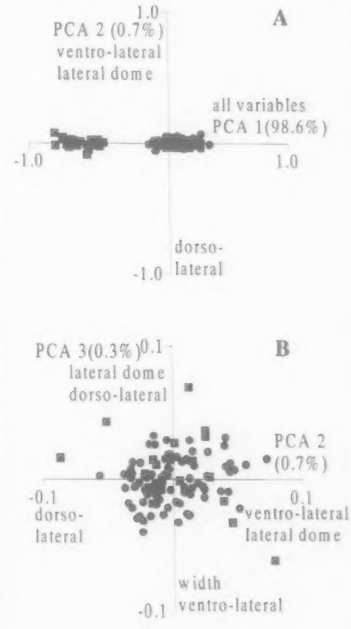


Figure 6

Relative growth of the length of statolith dimensions. Principal component scores for the length of five statolith dimensions on the first three axes. The percentages indicate how much variation in the data set has been described by each principal component axis. Data are $\log_{10}$ transformed. Circles = adults; squares = juveniles.

Additional variation in statolith shape described on the second and third PCA axes was attributable to differences among juvenile, rather than adult squid (Fig. 6, A and B: Table 4). Growth of the statolith along the ventrolateral and lateral dome axes and in total length were all important as statoliths approached their final size and shape. The ventrolateral and total lengths were proportionally larger in juveniles, whereas the dorsolateral length and total width were proportionally smaller immediately before individual statoliths attained their final adult shape.

If the PCA score of each individual statolith on the first axis, as a descriptor of shape, is used to estimate age of the squid, then an improved correlation between age and statolith shape is seen when compared to the correlation between age and statolith total length alone (juveniles n=15, r^2=0.73; adults n=61, r^2=0.61) (Fig. 4B). There is an exponential relationship for both juvenile and adult squid but changes in statolith shape slow in older individuals. Analysis of adult and juvenile statoliths as separate groups to eliminate gross statolith size differences that were identified in the PCA only highlighted the overall variability in statolith shape within the two age groups, particularly among adult squid.

Discussion

Results from this study suggest that neither statolith total length nor weight measurements can be reliably used to predict the age of a *Sepioteuthis lessoniana* individual. Statolith total length is a reasonable predictor of age for juvenile squid (less than 60 days old) but cannot be used to predict age in older individuals of this species. This conclusion is in contrast with that of González et al. (1996) who observed that statolith length in *Illex coindetti* shows significant dependence on age (males n=170, r^2=0.71; females n=171, r^2=0.74). However, they also suggested that the use of statolith length for age estimations would require verification over several years to confirm this relationship. Statolith length has also been shown to reflect age in *Illex illecebrosus* females (n=31, r^2=0.96) (Morris and Aldrich, 1985), whereas statolith weight provided a better reflection of age (n=112, r^2=0.88) than statolith total length in *Todarodes angolensis* (Villanueva, 1992). Even combining all five statolith dimensions to produce a description of statolith shape in this study provided only marginally better age estimates for *S. lessoniana* individuals than statolith total length or weight measurements alone.

Variation was evident in size between adult statoliths in this study because the heaviest statoliths did not necessarily possess the longest total lengths. Additionally, as much as half of the variation in statolith total lengths was not attributable to age of the

individuals. This indicates a disassociation between statolith and somatic (mantle length) growth in *S. lessoniana*. The disassociation of otolith and somatic growth has been demonstrated in several fish species (e.g. Mosegaard et al., 1988; Secor and Dean, 1989; Francis et al., 1993). In squids, *Loligo chinensis* (Jackson, 1995), and *Todaropsis eblanae* and *Todarodes angolensis* (Lipinski et al., 1993) also display disassociation between statolith and somatic tissue growth. Comparison of statolith size and shape between *Todarodes angolensis* and *Todaropsis eblanae* also has revealed distinct species differences (Lipinski et al., 1993). Jackson (1995) suggested that the use of the relation of statolith length to mantle length as a predictor of squid ages should proceed with caution until temperature-related effects on squid growth (e.g. seasonal effects), as well as the relation between statolith and somatic growth are better understood.

The disassociation between statolith and somatic growth rates is possibly a function of differences between the mechanisms responsible for these two processes. A process related to metabolic rate, rather than somatic growth, seems to govern the rate of otolith accretion in fish (Wright, 1991). Although a close correlation often exists between fish somatic growth and metabolic rate in early life-history stages, intrinsic or extrinsic constraints on somatic growth may affect this relationship and result in a disassociation between otolith and somatic growth (Wright, 1991). Recently, Lombarte and Lleonart (1993) proposed that otolith growth in fish may occur under dual regulation: overall shape is genetically determined whereas otolith size is governed by environmental factors. Several workers have also suggested that temperature plays a particularly important role in determining otolith growth, primarily through the effect of temperature on metabolic rate (Wright, 1991; Bradford and Geen, 1992). In order to demonstrate a link between otolith and somatic growth rates the age-independent variability in the relationship needs to be assessed (Hare and Cowen, 1995). The mechanisms governing statolith growth in *S. lessoniana* remain to be determined but may possibly be related to the high plasticity of somatic growth and a fixed growth trajectory of the statolith. Ontogenetic behavioral adaptations may also play a key role. Nonetheless, there are important considerations for age and growth studies based on the morphological features of statoliths; whereas many squid are known to grow continuously throughout their life (Jackson and Choat, 1992; Jackson, 1994), growth of statoliths in our study appears to approach a final asymptotic size and shape. Statoliths grow with the age of the squid, but statolith accretion may respond differently to environmental factors than to growth of somatic tissue.

The breakdown in the relation between statolith total length and age in older *S. lessoniana* individuals may be attributed to variable accretion rates in the statoliths of adult squid, possibly in relation to environmental conditions. Varying aragonite accretion within statoliths could bring about fluctuations in daily increment widths that ultimately lead to differences in overall length and weight of similar aged statoliths. These differences are likely to be more detectable in the older, larger statoliths of adult squid. Alterations in otolith increment widths leading to different sized otoliths of the same age have been shown for several fish species in response to both biotic and abiotic factors (e.g. Eckmann and Rey, 1987; Sogard, 1991; Burke et al., 1993). Further work on other fish species has shown that changes in increment width may lag or be unrelated to changes in somatic growth (Molony and Choat, 1990; Milicich and Choat, 1992). Variable statolith increment widths, that may be attributable to environmental conditions, have been shown in at least one squid species (*Abralia trigonura*, Bigelow, 1992), and one cuttlefish (*Sepia hierredda*, Raya et al. 1994).

Modifications of otolith shape and daily increment structure in fish have been attributed to environmental changes or fluctuations in individual fish physiology (Morales-Nin, 1987; Nishimura, 1993; Wright, 1993; Tzeng and Tsai, 1994). As some fish migrate, modifications are often necessary in order to meet unique requirements for balance, orientation, and navigation (Blaxter, 1988). A transformation of otolith shape may occur, resulting in discontinuities and secondary growth structures (Sogard, 1991; Hare and Cowen, 1994). Statoliths are the major sensory structure responsible for balance and orientation of squid (Budelmann, 1990). The shape and structure of the statocyst chamber itself are important to the swimming performance and sensory perception capabilities of cephalopods (Williamson, 1991). Statolith shape and structure is, therefore, also likely to affect the response of this unique and complex sensory organ. Although *S. lessoniana* does not display distinct life-style changes or habitat shifts, a transition from the observed juvenile habitat, where it commonly shelters among floating surface debris, to an adult lifestyle that is typically more reef-associated, may involve behavioral adaptations that lead to differential growth of statoliths. Knowledge of the mechanism by which this growth occurs and how it can be modified during ontogeny will be critical to understanding how statoliths grow.

Most growth of adult statoliths in this study occurred in the dorsal and lateral dome regions, producing a more rounded and bulkier form than that of the juveniles. The negative allometric growth in

total length and along the lateral dome and ventrolateral length axes suggests that relative growth of these regions is slow and that statoliths retain the elongate region of the rostrum as they grow. This was reflected in the superior definition and clarity of daily increment structures in the lateral dome region of adult statoliths when viewed under a light microscope. This may also explain why optical acuity of daily increment structures in the rostrum region of adult statoliths was poor. Slower growth of statoliths in the rostrum indicates deposition of less aragonite material compared with other faster growing regions of the statolith and in turn suggests that daily increment widths in the rostrum will be narrower and therefore harder to discern with light microscopy. In contrast, daily growth increments have been reported as displaying optimal definition in the rostrum of two other squid species (*Photololigo edulis*, Natsukari et al., 1988; *Berryteuthis magister*, Natsukari et al., 1993). Therefore, it is likely that differences occur in statolith accretion between species, possibly related to behavior. Optical definition of daily increments in statoliths has important consequences when ageing and growth studies are based on counts and distances between increments. Age and growth calculations based on narrower less distinct increments may not reveal true patterns otherwise evident in optically more distinct incrementation.

Results from this study suggest that prediction of age of *S. lessoniana* individuals from the size and shape of their statoliths remains doubtful on account of the disassociation between statolith and somatic tissue growth. Changes in statolith shape during growth may also be important if statoliths are to be employed as a tool for constructing growth histories of *S. lessoniana*. Variable levels of statolith accretion ultimately leading to slight modifications in shape may not necessarily be indicative of changes in somatic growth. Ageing studies based on analyses of statolith size from other squid species need to be aware of the possible disassociation between statolith and somatic tissue growth. The changes in size and shape of *Sepioteuthis lessoniana* statoliths described in this study are likely due to differing aragonite accretion levels, possibly on a daily basis, in response to physiological and behavioral adaptations during ontogeny.

Acknowledgments

We thank G. Jackson for providing constructive reviews of early manuscripts. We also acknowledge J. Semmens, G. Pecl, and P. Martinez for their assistance in the field and laboratory. This research was completed in partial fulfillment of an Honours degree by RT and was supported by a Merit Research Grant from James Cook University awarded to NAM.

Literature cited

Arkhipkin, A.
1993. Statolith microstructure and maximum age of *Loligo gahi* (Myopsida: Loliginidae) on the Patagonian Shelf. J. Mar. Biol. Assoc. U.K. 73:979–982.

Bigelow, K. A.
1992. Age and growth in paralarvae of the mesopelagic squid *Abralia trigonura* based on daily growth increments in statoliths. Mar. Ecol. Prog. Ser. 82:31–40.
1994. Age and growth of the oceanic squid *Onychoteuthis borealijaponica* in the North Pacific. Fish. Bull. 92:13–25.

Blaxter, J. H. S.
1988. Sensory performance, behaviour and ecology of fish. *In* J. Atema, R. R. Fay, A. N. Popper, and W. N. Tauolga (eds.), Sensory biology of aquatic animals. Springer-Verlag, New York, NY, p. 203–232.

Boehlert, G. W.
1985. Using objective criteria and multiple regression models for age determination in fish. Fish. Bull. 83:103–117.

Bradford, M. J., and G. H. Geen.
1992. Growth estimates from otolith increment widths of juvenile chinook salmon (*Oncorhynchus tshawytscha*) reared in changing environments. J. Fish Biol. 41:825–832.

Budelmann, B. U.
1990. The statocysts of squid. *In* D. L. Gilbert, W. J. Adelman Jr., and J. M. Arnold (eds.), Squid as experimental animals, p. 421–436. Plenum Press, London.

Burke, J. S., D. S. Peters, and P. J. Hanson.
1993. Morphological indices and otolith microstructure of Atlantic croaker, *Micropogonias undulatus*, as indicators of habitat quality along an estuarine pollution gradient. Environ. Biol. Fishes 36:25–33.

Campana, S. E., and J. D. Neilson.
1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42:1014–1032.

Clarke, M. R.
1978. The cephalopod statolith—an introduction to its form. J. Mar. Biol. Assoc. U.K. 58:701–712.

Eckmann, R., and P. Rey.
1987. Daily increments on the otoliths of larval and juvenile *Coregonus* spp., and their modification by environmental factors. Hydrobiologia 148:137–143.

Fletcher, W. J.
1991. A test of the relationship between otolith weight and age for the pilchard *Sardinops neopilchardus*. Can. J. Fish. Aquat. Sci. 48:35–38.

Forsythe, J. W.
1993. A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. *In* T. Okutani, R. K. O'Dor, and T. Kubodera (eds.), Recent advances in cephalopod fisheries biology, p. 133–143. Tokai Univ. Press, Tokyo.

Forsythe, J. W., and R. T. Hanlon.
1989. Growth of the eastern Atlantic squid, *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda). Aquacult. Fish. Manage. 20:1–14.

Francis, M. P., M. W. Williams, A. C. Pryce, S. Pollard, and S. G. Scott.
1993. Uncoupling of otolith and somatic growth in *Pagrus auratus* (Sparidae). Fish. Bull. 91:159–164.

González, A. F., B. G. Castro, and A. Guerra.
1996. Age and growth of the short-finned squid *Illex coindetti* in Galician waters (NW Spain) based on statolith analysis. ICES J. Mar. Sci. 53:802–810.

Hare, J. A., and R. K. Cowen.
1994. Ontogeny and otolith microstructure of bluefish *Pomatomus saltatrix* (Pisces: Pomatomidae). Mar. Biol. 118:541–550.
1995. Effect of age, growth rate, and ontogeny on the otolith size–fish size relationship in bluefish, *Pomatomus saltatrix*, and the implications for back-calculation of size in fish early life history stages. Can. J. Fish. Aquat. Sci. 52:1909–1922.

Jackson, G.D.
1990. Age and growth of the tropical near shore loliginid squid *Sepioteuthis lessoniana* determined from statolith growth ring analysis. Fish. Bull. 88:113–118.
1994. Application and future potential of statolith increment analysis in squids and sepioids. Can. J. Fish. Aquat. Sci. 51(11):2602–2626.
1995. Seasonal influences on statolith growth in the tropical nearshore loliginid squid *Loligo chinensis* (Cephalopoda: Loliginidae) off Townsville, North Queensland, Australia. Fish. Bull. 93:749–752.

Jackson, G. D., and J. H. Choat.
1992. Growth in tropical cephalopods: an analysis based on statolith microstructure. Can. J. Fish. Aquat. Sci. 49:218–228.

Jolicoeur, P.
1963. The multivariate generalisation of the allometry equation. Biometrics 19:497–499.

Jones, C.
1986. Determining age of larval fish with the otolith increment technique. Fish. Bull. 84:91–103.

Lipinski, M. R.
1986. Methods for the validation of squid age from statoliths. J. Mar. Biol. Assoc. U.K. 66:505–526.

Lipinski, M. R.
1993. The deposition of statolith—a working hypothesis. *In* T. Okutani, R. K. O'Dor, and T. Kubodera (eds.), Recent advances in cephalopod fisheries biology, p. 241–262. Tokai Univ. Press, Tokyo.

Lipinski, M. R., M. A. Compagno Roeleveld, and L. G. Underhill.
1993. Comparison of the statoliths of *Todaropsis eblanae* and *Todarodes angolensis* (Cephalopoda: Ommastrephidae) in South African waters. *In* T. Okutani, R. K. O'Dor, and T. Kubodera (eds.), Recent advances in cephalopod fisheries biology. Tokai Univ. Press, Tokyo, p. 263–273.

Lombarte, A., and J. Lleonart.
1993. Otolith size changes related with body growth, habitat depth and temperature. Environ. Biol. Fishes 37:297–306.

Marcus, L.
1990. Traditional morphometrics. *In* F. J. Rohlf and F. L. Bookstein (eds.), Proceedings of the Michigan morphometrics workshop, p. 77–122. Univ. Michigan Museum of Zoology, Special Publication 2

Milicich, M. J., and J. H. Choat.
1992. Do otoliths record changes in somatic growth rate? Conflicting evidence from a laboratory and field study of a temperate reef fish, *Parika scaber*. Aust. J. Mar. Freshwater Res. 43:1203–1214.

Molony, B. W., and J. H. Choat.
1990. Otolith increment widths and somatic growth rate: the presence of a time-lag. J. Fish Biol. 37:541–551.

Morales-Nin, B. Y. O.
1987. The influence of environmental factors on microstructure of otoliths of three demersal fish species caught off Namibia. S. Afr. J. Mar. Sci. 5:255–262.

Morris, C. C., and F. A. Aldrich.
1985. Statolith length and increment number for age determination of *Illex illecebrosus* (LeSueur, 1821) (Cephalopoda: Ommastrephidae). NAFO Scientific Council Studies 9:101–106.

Mosegaard, H., H. Svedang, and K. Taberman.
1988. Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. Can. J. Fish. Aquat. Sci. 45:1514–1524.

Mugiya, Y., and S. Tanaka.
1992. Otolith development, increment formation, and an uncoupling of otolith to somatic growth rates in larval and juvenile goldfish. Nippon Suisan Gakkaishi. 58:845–851.

Natsukari, Y. T., T. Nakanose, and K. Oda.
1988. Age and growth of loliginid squid *Photololigo edulis* (Hoyle, 1855). J. Exp. Mar. Biol. Ecol. 116:177–190.

Natsukari, Y., H. Mukai, S. Nakahama, and T. Kubodera.
1993. Age and growth estimation of a gonatid squid, *Berryteuthis magister*, based on statolith microstructure (Cephalopoda: Gonatidae). *In* T. Okutani, R. K. O'Dor, and T. Kubodera (eds.), Recent advances in cephalopod fisheries biology. p. 351–364. Tokai Univ. Press, Tokyo.

Nishimura, A.
1993. Occurrence of a check in otoliths of reared and sea-caught larval walleye pollock *Theragra chalcogramma* (Pallas) and its relationship to events in early-life history. J. Exp. Mar. Biol. Ecol. 166:175–183.

Radtke, R. L.
1983. Chemical and structural characteristics of statoliths from the short-finned squid *Illex illecebrosus*. Mar. Biol. 76:47–54.

Raya, C. P., M. M. Fernandez-Nunez, E. Balguerias, and C. L. Hernandez-Gonzalez.
1994. Progress towards ageing cuttlefish (*Sepia hierredda*, Rang 1837) from North West African coast using statoliths. Mar. Ecol. Prog. Ser. 114:139–147.

Secor, D. H., and J. M. Dean.
1989. Somatic growth effects on the otolith-fish size relationship in young pond-reared striped bass, *Morone saxatilis*. Can. J. Fish. Aquat. Sci. 46:113–121.

Shea, B. T.
1985. Bivariate and multivariate growth allometry: statistical and biological considerations. J. Zool. Lond. 206:367–390.

Sogard, S. M.
1991. Interpretation of otolith microstructure in juvenile winter flounder (*Pseudopleuronectes americanus*): ontogenetic development, daily increment validation, and somatic growth relationships. Can. J. Fish. Aquat. Sci. 48:1862–1871.

Stevenson, D. K., and S. E. Campana (eds.).
1992. Otolith microstructure examination and analysis. Can. Spec. Publ. Fish. Aquat. Sci. 117, 126 p.

Tzeng, W. N., and Y. C. Tsai.
1994. Changes in otolith microchemistry of the Japanese eel, *Anguilla japonica*, during its migration from the ocean to the rivers of Taiwan. J. Fish Biol. 45:671–683.

Villanueva, R.
1992. Interannual growth differences in the oceanic squid *Todarodes angolensis* Adam in the northern Benguela upwelling system, based on statolith growth increment analysis. J. Exp. Mar. Biol. Ecol. 159:157–177.

Williamson, R.
1991. Factors affecting the sensory response characteris-

tics of the cephalopod statocyst and their relevance in predicting swimming performance. Biol. Bull. 180:221–227.

Wright, P. J.

1991. The influence of metabolic rate on otolith increment width in Atlantic salmon parr, *Salmo salar* L. J. Fish Biol. 38:929–933.

1993. Otolith microstructure of the lesser sandeel, *Ammodytes marinus*. J. Mar. Biol. Assoc. U.K. 73:245–248.

Wright, P. J., N. B. Metcalfe, and J. E. Thorpe.

1990. Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L: evidence against coupling. J. Fish. Biol. 36:241–249.

Differential habitat use by California halibut, *Paralichthys californicus*, barred sand bass, *Paralabrax nebulifer*, and other juvenile fishes in Alamitos Bay, California

Charles F. Valle

John W. O'Brien

Kris B. Wiese

California Department of Fish and Game
330 Golden Shore, Suite 50
Long Beach, California 90802
E-mail address (for C. F. Valle): cvalle@dfg2.ca.gov

Abstract.—Economically valuable California halibut, *Paralichthys californicus*, and barred sand bass, *Paralabrax nebulifer*, along with other fishes, are often abundant in the shallow areas of California bays during their early life history. However, little is known about their habitat use within these areas. We investigated habitat use of juvenile fishes in the shallow waters of an embayment by towing a 1.6-m beam trawl with 3-mm mesh through eelgrass beds (*Zostera marina*) and unvegetated areas at depths ≤1.1 m in Alamitos Bay. Tows were conducted monthly or bimonthly from May 1992 through November 1995. A total of 435 tows during 31 months yielded 52,787 fishes comprising 46 species. However, the catch was dominated by only a few species and consisted mostly of juveniles and gobiid larvae. A total of 1157 California halibut and 225 barred sand bass were collected. California halibut were 2–6 times more abundant in unvegetated areas than in eelgrass beds, whereas barred sand bass were captured almost exclusively in eelgrass. Abundance of both species significantly decreased as distance from the bay mouth increased. Abundances of most other fishes also varied considerably between habitats and among sites. In contrast to California halibut and barred sand bass, abundances of other species were higher at sites farther inside the bay. Variations in water temperature, dissolved oxygen, salinity, eelgrass shoot density, and eelgrass blade length failed to explain differences in abundance for most fishes. Habitat and site selection for juvenile California halibut and barred sand bass may be related to larval supply and to the first suitable area encountered, but may be modified subsequently by movement into other areas in search of preferred food items.

Manuscript accepted 25 June 1998.
Fish. Bull. 97:646–660 (1999).

It is widely recognized that bays and estuaries are important nursery grounds for many marine species. Within these areas, numerous studies have documented the importance of eelgrass, *Zostera marina*, and other seagrasses as habitat for fishes. The composition and abundance of fishes in these habitats can vary considerably from unvegetated areas (Orth and Heck, 1980; Borton, 1982; reviewed in Orth et al., 1984; Heck et al., 1989; Ferrell and Bell, 1991; Sogard and Able, 1991). Seagrass habitats may be important because of their associated food resources or because they provide a refuge from predation (Adams, 1976; Heck and Thoman, 1981; reviewed in Orth et al., 1984; Leber, 1985; Sogard and Olla, 1993).

The association of fishes with seagrass beds has been related to various physical characteristics of seagrass, such as shoot density, blade length, and biomass (Adams, 1976; Orth and Heck, 1980; reviewed in Orth et al., 1984; Bell and Westoby, 1986a). However, evidence suggests that physical characteristics of seagrasses may only affect fish abundances on a local scale such as within a seagrass bed, but not over larger scales such as different beds within a bay (Bell and Westoby, 1986b; Bell et al., 1988; Sogard, 1989; Worthington et al., 1992). Instead, it has been suggested that differing fish abundances in seagrass beds across an estuary are due to availability of competent larvae; pelagic larvae of some seagrass fishes settle indiscriminately in the first seagrass bed encountered regardless of seagrass physical characteristics (Bell and Westoby, 1986b; Bell et al., 1987, 1988). According to this "settle and stay" hypothesis, once within a seagrass bed, fishes would move around selecting microsites but would not leave the seagrass bed because of greater predation risks associated with moving over unvegetated substrata. However, others have found that initial settlement patterns in habitats may be altered considerably by postsettlement mortality (Levin, 1994), migration to other areas (Sogard, 1989), or by both in response to available food (Jenkins et al., 1996).

Much of the work on seagrasses and associated fishes has taken place on the east coast of the United States or in other parts of the world. Although several studies have described the ichthyofauna of southern California bays (Allen and Horn, 1975; Horn and Allen, 1976; Allen, 1982; Allen and Herbinson, 1991), few studies have described the relation of fishes with eelgrass and other habitats. Understanding

these relationships within bays is particularly important owing to the destruction and severe alteration of about 75% of coastal estuary and wetland habitats in southern California since 1900 (California Coastal Zone Conservation Commissions, 1975). Reduced catches of California halibut, *Paralichthys californicus*, may be due to the alteration or loss of this nursery habitat within bays and estuaries, or to both (Plummer et al., 1983; Kramer and Sunada, 1992; Kramer and Hunter[1]).

California halibut is an important commercial and sport fish in southern and central California. Barred sand bass, *Paralabrax nebulifer*, is also an important sport fish in southern California and ranks annually among the top three species caught aboard commercial passenger fishing vessels (Love et al., 1996a). Both of these fishes spawn in nearshore waters (Frey, 1971; Ono, 1992) and occupy embayments during their early life history; newly settled and larger juvenile California halibut are frequently found over shallow, sandy substrata (Haaker, 1975; Allen, 1988; Allen and Herbinson, 1990, 1991; Kramer, 1990, 1991a, 1991b), whereas juvenile barred sand bass are found in eelgrass beds (Feder et al., 1974; Rosales-Casián, 1997). However, little additional information is available on habitat use by these and other fishes within these areas.

Therefore, the purpose of our study was to determine 1) if abundances of juvenile California halibut, barred sand bass, and other fishes differed between eelgrass and unvegetated habitats, 2) whether these abundances differed among sites within the bay, and 3) whether these differences were related to physical characteristics of eelgrass or abiotic factors. We examined habitat use by collecting fishes with a beam trawl towed in shallow eelgrass beds and nearby unvegetated areas at three sites within a single bay. A beam trawl was used because it collects smaller halibut and other flatfishes more effectively than beach seines and otter trawls (Gunderson and Ellis, 1986; Kramer, 1990; Kuipers et al., 1992) and allows comparison with other studies where similar gear was used.

Materials and methods

Study area and sampling

Our study was conducted in Alamitos Bay (lat. 33°45'N, long. 118°07'W), which is a small embayment located at the southeastern boundary of Los Angeles County in southern California. Alamitos Bay was once an estuary of tidal marshes and mud flats. It has been considerably modified by dredging, filling, and construction of homes, marinas, and two jetties that mark the entrance. The bay is exposed to semidiurnal tides with a mean range of 1.1 m. Water circulation is further enhanced by large amounts of water drawn by two power stations that flush the bay every 19 hours (Phillips[2]). Regardless of tidal flux, there is a consistent flow of water into the bay (Brown and Caldwell[3]).

Sampling was conducted at three sites (Bay Entrance, Belmont Shore, and Marine Stadium) separated by at least one km (Fig. 1). At each site, sampling occurred in two habitats, eelgrass (*Zostera marina*) beds and nearby unvegetated sandy-mud areas located about 40 m away. A weighted 1.6-m beam trawl, equipped with skis, tickler chain, and 3.0-mm stretched-mesh netting, was towed parallel to shore by two people on foot at low tide during the lowest tides of the month. Tows were made during daylight hours at depths from 0.3 m to 1.1 m, lasted 90 seconds, and covered approximately 56 m^2. We completed 2–5 tows, depending on tide height, in each habitat at each site over four consecutive days. Sampling was conducted monthly from May 1992 through April 1993 (excluding February) and from November 1993 through December 1994. Bimonthly sampling occurred from January 1995 through November 1995. All fishes were sorted, identified, counted, and returned to the water. Most fishes were measured to the nearest mm standard length (SL) from May 1992 through October 1994, whereas California halibut and barred sand bass were measured throughout the study. Although California halibut and barred sand bass undergo transformation at about 7–9 mm SL and 11 mm SL, respectively (Butler et al., 1982; Ahlstrom et al., 1984; Gadomski et al., 1990), all individuals ≤20 mm SL were considered to be "newly settled" or "newly recruited" (Allen and Herbinson, 1990; Kramer, 1990; Love et al., 1996b). Larval and postlarval gobies (Brothers, 1975) that were not identified further were classified as "goby larvae." Other fishes not sexually mature based on size at first maturity information were considered to be juveniles. Water temperature, dissolved oxygen, and salinity data were collected for most tows,

[1] Kramer, S. H., and J. R. Hunter. 1987. Southern California wetland/shallow water habitat investigation. Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038. Ann. Rep. for Fiscal Year 1987, 12 p.

[2] Phillips, K. W. 1978. A water and sediment study of Alamitos Bay correlated with peak and minimal recreational aquatic activities. City of Long Beach Chemical and Physical Testing Laboratory, Long Beach, California. Unpubl. data.

[3] Brown and Caldwell Environmental Sciences Division. 1979. Embayment ecology studies: physical oceanographic and water quality data report. Southern California Edison. Unpubl. data.

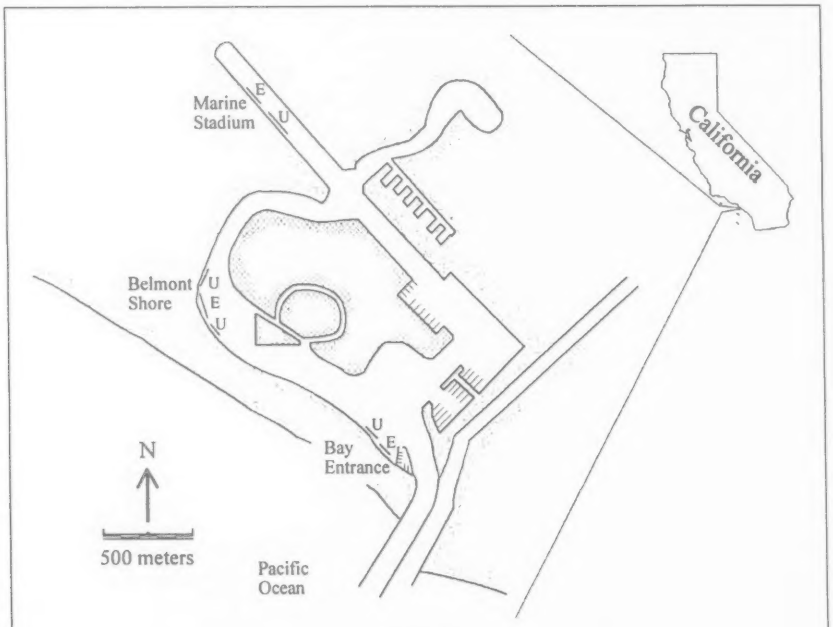


Figure 1

Location of sampling sites (Bay Entrance, Belmont Shore, and Marine Stadium) in Alamitos Bay, California. U=unvegetated habitats, E=eelgrass habitats.

except during September 1994 through December 1994, when dissolved oxygen values were not taken owing to equipment failure. Bottom water temperature and dissolved oxygen were recorded with a YSI Model 51B oxygen meter. Surface salinity was measured with a temperature-compensated refractometer.

Eelgrass bed length, bed width, shoot density, and blade lengths were measured by two divers using SCUBA. A 300-m transect tape was laid out in the center of the bed along its longest axis. Width was measured perpendicular to the tape at three equidistant points. Divers sampled 1/16 m^2 quadrats in the bed at predetermined random points perpendicular to the tape. Within each quadrat, all shoots were counted and the lengths of two randomly selected blades were measured. A total of 10–20 quadrats were sampled at each site during August 1992, March 1993, December 1993, and December 1995.

Data analysis

Nonparametric statistics were used because data and their transformations were heteroscedastic and not normally distributed. A nonparametric two-factor analysis of variance (ANOVA) on ranked data (Zar, 1984) was performed separately on the number of California halibut, barred sand bass, and 13 other common fishes captured per tow with habitat and site as factors. If significant main effects with no significant interactions were found, Tukey-Kramer multiple comparisons were performed to determine which pairs of means were significantly different. The results were considered significant if P was <0.05. If significant interactions between habitat and site were found, analyses of main effects were considered dubious and subsets of data were formed for each level of one factor within each level of the other factor and *vice-versa* (Underwood, 1981). Kruskal-Wallis and Dunn multiple comparisons (Hollander and Wolfe, 1973) were performed on these subsets. For example, a Kruskal-Wallis test was used to determine if there was an overall difference in abundance among sites for unvegetated habitats, and then for eelgrass habitats. If a significant difference was found, Dunn multiple comparisons were made to determine which pairs of sites were significantly different. For fishes other than California halibut and barred sand bass, comparisons among sites were made only for the habitat where they were most abundant overall. Abundance differences between habitats were determined by a Wilcoxon two-sample test on unvegetated and eelgrass habitat data within each site.

Two-sample Kolmogorov-Smirnov tests were used to compare length-frequency distributions between

Table 1

Physical characteristics of eelgrass (*Zostera marina*) at three sites in Alamitos Bay. Data were collected in August 1992, March 1993, December 1993, and December 1995. Values represent mean ± one standard error. Sample sizes for bed length and width measurements were 4 and 12, respectively. Sample sizes for density: Bay Entrance=79, Belmont Shore=70, and Marine Stadium=80. Sample sizes for blade length: Bay Entrance=154, Belmont Shore=138, and Marine Stadium=155.

Site	Bed length (m)	Bed width (m)	Density (no. shoots per quadrat)	Blade length (cm)
Bay Entrance	82.9 ± 18.6	16.3 ± 2.9	10.1 ± 0.5	68.3 ± 2.2
Belmont Shore	102.9 ± 2.5	8.8 ± 0.3	7.9 ± 0.5	37.2 ± 1.5
Marine Stadium	54.1 ± 5.9	15.8 ± 1.3	10.6 ± 0.7	47.9 ± 1.9

habitats and sites for California halibut and barred sand bass. Subsets of these data (see above) were used in these analyses.

Kruskal-Wallis and Dunn multiple comparisons were also made on the mean number of eelgrass shoots and mean blade length per quadrat to determine differences in these eelgrass characteristics among the three sites. Water temperature, dissolved oxygen, and salinity values for each tow were used in a two-way nonparametric ANOVA to test for differences in each of these abiotic factors between habitats and among sites.

Results

Eelgrass characteristics and abiotic factors

Physical characteristics of eelgrass beds at the three sites were very different. Belmont Shore had the longest bed but mean bed width, eelgrass shoot density, and eelgrass blade length were lowest (Table 1). Eelgrass densities at Bay Entrance and Marine Stadium were significantly greater than at Belmont Shore ($P<0.05$), and all blade length comparisons among sites were significantly different ($P<0.05$).

Abiotic factors varied temporally but showed little spatial variation. Mean monthly values ranged from 14.5 to 23.0°C for water temperature, 4.8–8.1 mg/L for dissolved oxygen, and 23.2–36.0 ppt for salinity. These abiotic factors were very similar between habitats and among sites except for slightly lower dissolved oxygen in eelgrass and higher water temperatures at Marine Stadium. However, none of these abiotic factors were significantly different between habitats or among sites ($P>0.05$).

Fish community

A total of 52,787 fish representing 46 species was collected from 435 tows (Table 2). The catch was dominated by a few species that were often captured in large numbers.

Numbers of species varied among habitats and sites. Many more species were captured in eelgrass beds ($n=42$) than in unvegetated areas ($n=26$). We collected 19 species exclusively in eelgrass beds but captured only three species solely in unvegetated areas (Table 2). Species numbers decreased as distance from the bay mouth increased; more species were collected at Bay Entrance ($n=40$) than at Belmont Shore ($n=35$) and Marine Stadium ($n=28$).

California halibut

California halibut ranked eighth in abundance; 1157 individuals were collected from 50.8% of the tows (Table 2). The number of California halibut captured per tow ranged from 0 to 81 with a mean of 2.7 ± 0.32 SE. The abundance of newly settled California halibut was greatest from March through May (Fig. 2). A total of 325 newly settled California halibut was captured. For all sites and habitats combined, maximum mean density per month of newly settled individuals was 15/100 m^2 (May 1995). Maximum mean density per month at an individual site and habitat was 81/100 m^2 (May 1995, Bay Entrance unvegetated area).

California halibut abundance varied considerably among habitats and sites (Fig. 3A). The magnitude of these differences depended upon the habitat and site as indicated by a significant interaction term in the two-way ANOVA ($P=0.002$). Abundance was significantly different between habitats at all three sites, for all three site comparisons in unvegetated areas, and for two of three comparisons in eelgrass beds (Table 3). Within sites, Marine Stadium and Belmont Shore unvegetated areas contained about 2–3 times as many California halibut as eelgrass beds, and Bay Entrance unvegetated area had more than six times as many California halibut as nearby eelgrass (Fig. 3A). Within both habitats, California

Table 2

Total number of fishes captured by habitat type and frequency of occurrence in Alamitos Bay, California, from May 1992 through November 1995.

Common name	Scientific name	Unvegetated habitat n=251	Eelgrass habitat n=184	Total number captured	Frequency of occurrence (%) n=435
Goby larvae	unidentified Gobiidae	6491	10336	16827	57.7
Cheekspot goby	*Ilypnus gilberti*	8836	1009	9845	74.9
Bay pipefish	*Syngnathus leptorhynchus*	70	8203	8273	49.0
Shiner perch	*Cymatogaster aggregata*	5	4121	4126	23.2
Topsmelt	*Atherinops affinis*	2463	1163	3626	33.1
Giant kelpfish	*Heterostichus rostratus*	9	2454	2463	36.8
Arrow goby	*Clevelandia ios*	1216	840	2056	18.6
California halibut	*Paralichthys californicus*	1024	133	1157	50.8
Queenfish	*Seriphus politus*	662	253	915	13.1
Diamond turbot	*Hypsopsetta guttulata*	625	53	678	37.9
Spotted kelpfish	*Gibbonsia elegans*	1	478	479	19.3
Shadow goby	*Quietula y-cauda*	20	394	414	12.9
Pacific staghorn sculpin	*Leptocottus armatus*	241	129	370	37.0
Bay blenny	*Hypsoblennius gentilis*	3	326	329	20.5
Barred sand bass	*Paralabrax nebulifer*	4	221	225	12.4
Salema	*Xenistius californiensis*	0	180	180	4.6
California killifish	*Fundulus parvipinnis*	42	128	170	8.5
Black perch	*Embiotoca jacksoni*	0	86	86	5.3
Sargo	*Anisotremus davidsonii*	0	86	86	3.7
Spotted turbot	*Pleuronichthys ritteri*	54	12	66	8.7
Kelp bass	*Paralabrax clathratus*	0	56	56	6.7
Snubnose pipefish	*Cosmocampus arctus*	2	46	48	7.4
California clingfish	*Gobiesox rhessodon*	4	41	45	5.1
Black croaker	*Cheilotrema saturnum*	0	42	42	4.4
Mussel blenny	*Hypsoblennius jenkinsi*	7	35	42	3.9
Spotted sand bass	*Paralabrax maculatofasciatus*	0	38	38	4.6
Reef finspot	*Paraclinus integripinnis*	0	30	30	3.2
Dwarf surfperch	*Micrometrus minimus*	0	28	28	2.5
Yellowfin goby	*Acanthogobius flavimanus*	8	8	16	2.8
Mozambique tilapia	*Tilapia mossambica*	0	14	14	2.1
Blenny larvae	*Hypsoblennius* spp.	0	9	9	1.2
California tonguefish	*Symphurus atricauda*	3	5	8	1.4
California scorpionfish	*Scorpaena guttata*	0	6	6	1.2
Senorita	*Oxyjulis californica*	0	4	4	0.9
White seabass	*Atractoscion nobilis*	1	3	4	0.7
Bonefish	*Albula vulpes*	2	2	4	0.5
Unidentified larvae	unidentified Teleosti	4	0	4	0.5
Opaleye	*Girella nigricans*	0	3	3	0.7
Rockpool blenny	*Hypsoblennius gilberti*	0	3	3	0.2
Pacific sardine	*Sardinops sagax*	2	0	2	0.5
Pile perch	*Rhacochilus vacca*	0	2	2	0.5
Anchovy larva	unidentified Engraulidae	1	0	1	0.2
Chocolate pipefish	*Syngnathus euchrous*	0	1	1	0.2
Hornyhead turbot	*Pleuronichthys verticalis*	0	1	1	0.2
Longjaw mudsucker	*Gillichthys mirabilis*	0	1	1	0.2
Pacific barracuda	*Sphyraena argentea*	1	0	1	0.2
Rock wrasse	*Halichoeres semicinctus*	0	1	1	0.2
Striped mullet	*Mugil cephalus*	1	0	1	0.2
White seaperch	*Phanerodon furcatus*	0	1	1	0.2

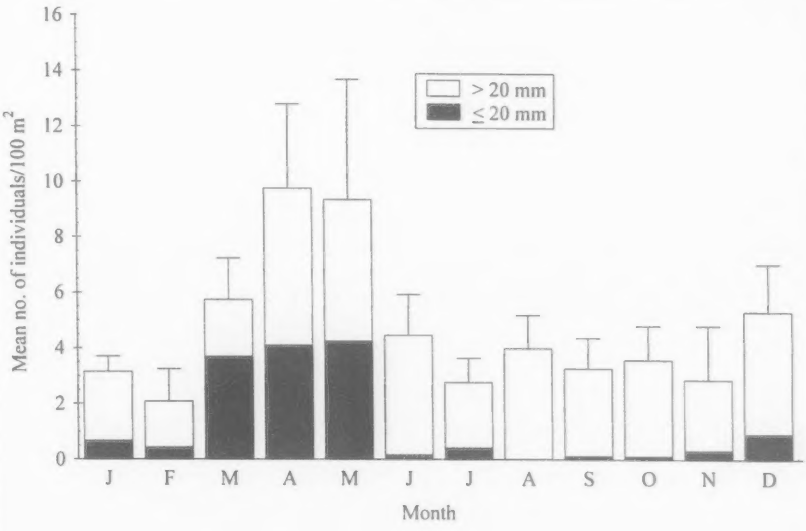


Figure 2

Mean number per 100 m^2 of newly settled (≤20 mm SL) and larger California halibut (*Paralichthys californicus*) captured by month in Alamitos Bay from May 1992 through November 1995 (n=435 tows). Error bars represent + one standard error for the total number of halibut per 100 m^2 captured by month.

halibut abundance decreased as distance from the bay mouth increased. Within unvegetated areas, California halibut were approximately 6 and 14 times more abundant at Bay Entrance than at Belmont Shore and Marine Stadium, respectively.

California halibut length ranged from 7 to 253 mm SL, but few were larger than 140 mm SL; no adults were captured. Lengths were similar among habitats and sites except that many more newly settled individuals were captured in unvegetated areas than in eelgrass beds, particularly at Bay Entrance (Fig. 4). The length-frequency distribution of California halibut in unvegetated habitat at Bay Entrance was significantly different from nearby eelgrass (P=0.007) and from Belmont Shore unvegetated area (P=0.001). No other length-frequency comparisons were significantly different (P>0.05).

Table 3

Results of Kruskal-Wallis test (KW) and Dunn multiple comparisons (D) of California halibut (*Paralichthys californicus*) abundance between habitats and among sites. df=degrees of freedom, H=Kruskal-Wallis statistic. BE=Bay Entrance, BS=Belmont Shore, MS=Marine Stadium, U=unvegetated habitat, and E=eelgrass (*Zostera marina*) habitat. *=significant at P<0.05.

Comparison	Test	df	Statistic	P-value
Habitat (U vs. E)				
BE	KW	1	H=55.58*	0.0001
BS	KW	1	H=16.03*	0.0001
MS	KW	1	H=5.80*	0.0161
Site (U)	KW	2	H=115.23*	0.0001
BE vs. BS	D		*	<0.05
BE vs. MS	D		*	<0.05
BS vs. MS	D		*	<0.05
Site (E)	KW	2	H=22.65*	0.0001
BE vs. BS	D		*	<0.05
BE vs. MS	D		*	<0.05
BS vs. MS	D			>0.05

Barred sand bass

We collected 225 barred sand bass from 12.4% of the tows (Table 2). The number of barred sand bass captured per tow ranged from 0 to 42 with a mean of 0.5 ± 0.14 SE. Newly recruited barred sand bass and most larger juveniles were captured from September through November (Fig. 5). Barred sand bass were captured almost exclusively (98.2%) in eelgrass beds and none were captured at Marine Stadium (Fig. 3B), leading to a significant interaction term in the two-way ANOVA (P=0.003). Because barred sand

bass were not captured at Marine Stadium and few were captured in unvegetated areas, only numbers within eelgrass beds at Bay Entrance and Belmont Shore were tested. Although approximately twice as many individuals were caught at Bay Entrance than at Belmont Shore, these results were not significantly different (P=0.68).

Lengths of barred sand bass ranged from 16 to 92 mm SL but most (66.2%) were ≤40 mm SL; no adults were captured. Average length at Bay Entrance (34.1 mm ±1.1 SE, n=156) was smaller than at Belmont Shore (43.5 mm ±1.4 SE, n=67), primarily due to the greater abundance of new recruits and small juveniles (21–30 mm SL) at Bay Entrance (Fig. 6). Length-frequency distributions of barred sand bass at these two sites were significantly different (P= 0.0001).

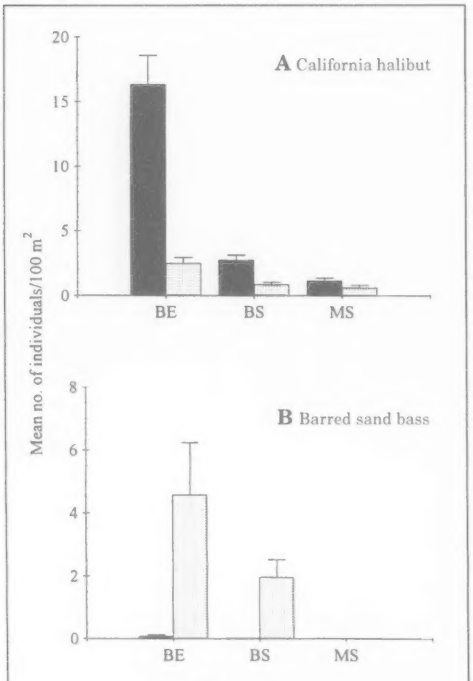


Figure 3

Mean number per 100 m² of (**A**) California halibut (*Paralichthys californicus*) and (**B**) barred sand bass (*Paralabrax nebulifer*) captured in unvegetated and eelgrass (*Zostera marina*) habitats at three sites in Alamitos Bay from May 1992 through November 1995. Dark bars represent unvegetated habitats and stippled bars represent eelgrass habitats. BE=Bay Entrance, BS=Belmont Shore, and MS=Marine Stadium. Number of tows in unvegetated habitats at BE, BS, and MS were 95, 61, and 95, respectively. Number of tows in eelgrass habitats at BE, BS, and MS were 60, 62, and 62, respectively. Error bars represent + one standard error.

Other species

Gobies were the most abundant group of fishes, accounting for 55.2% of the total (Table 2). This group comprised mostly arrow goby (*Clevelandia ios*), cheekspot goby (*Ilypnus gilberti*), and numerous goby larvae that were probably arrow goby and cheekspot goby. Bay pipefish (*Syngnathus leptorhynchus*), shiner perch (*Cymatogaster aggregata*), topsmelt (*Atherinops affinis*), and giant kelpfish (*Heterostichus rostratus*) were the other most abundant fishes, and along with gobies represented 87.9% of all individuals collected. These fishes, along with queenfish (*Seriphus politus*), diamond turbot (*Hypsopsetta guttulata*), spotted kelpfish (*Gibbonsia elegans*), shadow goby (*Quietula y-cauda*), Pacific staghorn sculpin (*Leptocottus armatus*), and bay blenny (*Hypsoblennius gentilis*), were considered "common fishes." The common fishes, along with California halibut and barred sand bass, accounted for 96.5% of the total number collected. Abundances for most of these fishes peaked from March through May or from June through August; most of these fishes were juveniles.

All of the common fishes were found in both habitats and at all sites; however the number of individuals varied considerably (Fig. 7). Only queenfish and Pacific staghorn sculpin had no significant interactions between habitat and site in the nonparametric two-factor ANOVA (P>0.05). Queenfish were significantly more abundant in unvegetated areas than in eelgrass beds (P=0.0003). No significant habitat differences were found for Pacific staghorn sculpin (P=0.41). Queenfish were significantly more abundant at Marine Stadium than at Belmont Shore (P<0.05), whereas Pacific staghorn sculpin were significantly more abundant at Belmont Shore than at Bay Entrance (P<0.05).

For 11 of the 13 common fishes, the nonparametric two-way ANOVA yielded significant interactions between habitat and site (P<0.05). Stratifying by site and comparing abundances between eelgrass and unvegetated areas, we found that bay pipefish, shiner perch, giant kelpfish, spotted kelpfish, shadow goby, and bay blenny were significantly more abundant in eelgrass than in unvegetated areas at all three sites (P<0.05). Cheekspot goby and diamond turbot were significantly more abundant in unvegetated areas than eelgrass at all three sites, whereas goby larvae and arrow goby were significantly more abundant in unvegetated areas at Belmont Shore (P<0.05).

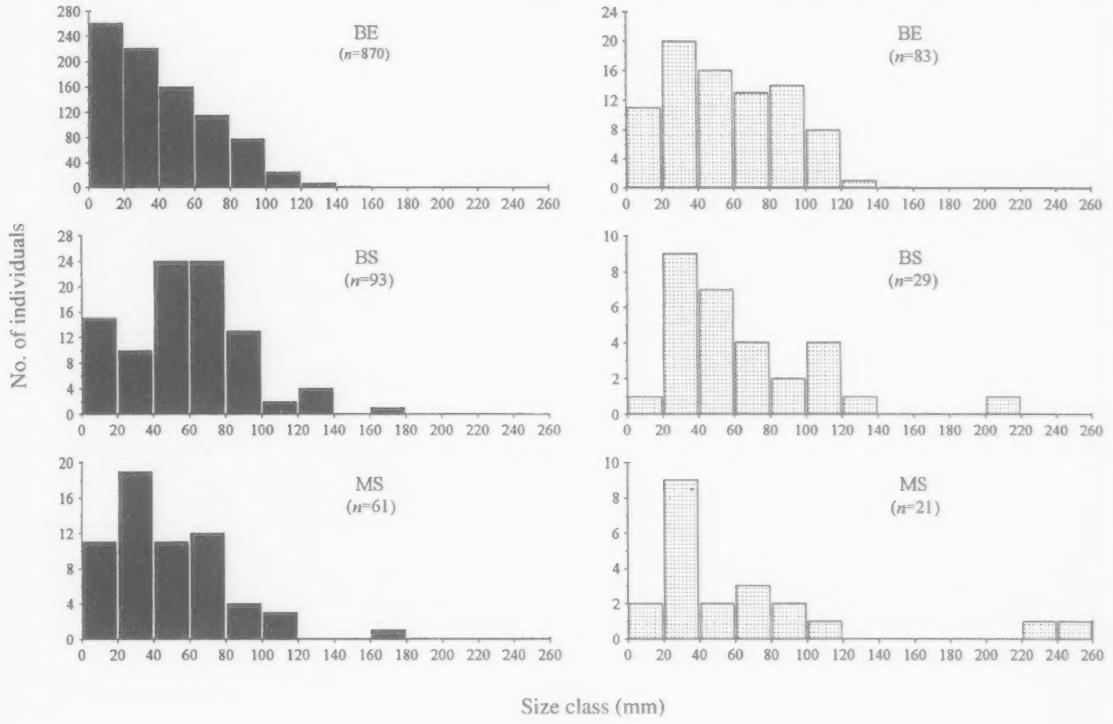


Figure 4

Length-frequency distributions of California halibut (*Paralichthys californicus*) captured in unvegetated and eelgrass (*Zostera marina*) habitats in Alamitos Bay from May 1992 through November 1995. Dark bars represent unvegetated habitats and stippled bars represent eelgrass habitats. See Figure 3 for further explanation.

Topsmelt showed a mixed pattern; they were significantly more abundant in eelgrass at Marine Stadium ($P<0.05$) but significantly more abundant in unvegetated area at Belmont Shore ($P<0.05$).

Stratifying by habitat and comparing abundances among sites, we found that most fishes were significantly more abundant at Marine Stadium or at Belmont Shore ($P<0.05$) (Table 4). Only shiner perch, giant kelpfish, and bay blenny had significantly more individuals at Bay Entrance than at one of the other two sites, but abundances at Bay Entrance were never significantly greater than at both of the other sites.

Discussion

California halibut and barred sand bass

Abundance of California halibut was habitat specific. California halibut was one of the few fishes whose abundance was much higher in unvegetated areas than in eelgrass beds. Although eelgrass blades may provide shelter from predation for some inhabitants (Heck and Thoman, 1981; Sogard and Olla, 1993), California halibut typically avoid detection by predators and prey by partially burying themselves in sediment (Haaker, 1975). Other flatfishes show substrate preferences (Tanda, 1990; Burke et al., 1991; Rogers, 1992), and California halibut ≤63 mm SL prefer bare sand over eelgrass in the laboratory (Drawbridge, 1990). Thus, sediments supporting eelgrass beds may not be preferable for settlement. It is also possible that eelgrass physically impedes halibut from settling there. If this were solely the case, then fewer halibut would be expected in eelgrass beds where distances between shoots were shorter (dense beds) than in beds where distances between shoots were greater (sparse beds). However, we found this not to be true; more halibut were found in a dense eelgrass bed (Bay Entrance) than in a sparse bed (Belmont Shore).

Barred sand bass abundance was also habitat specific; they were almost exclusively found in eelgrass

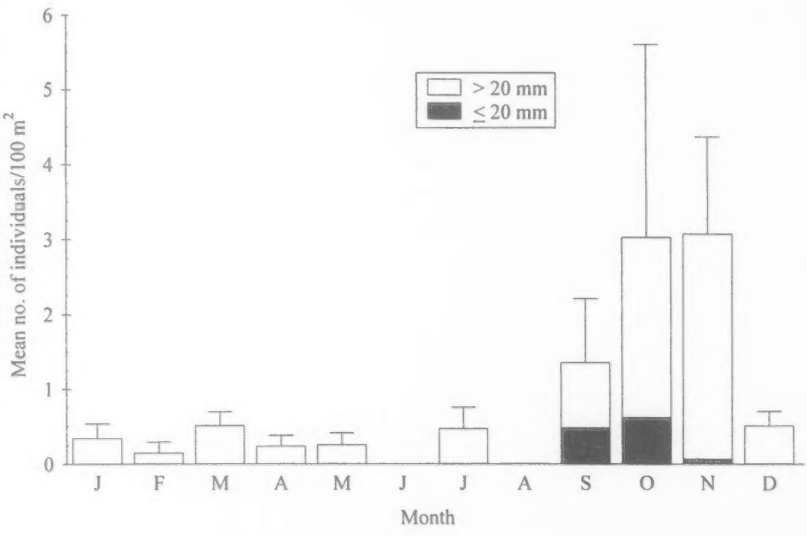


Figure 5

Mean number per 100 m^2 of newly recruited (≤20 mm SL) and larger barred sand bass (*Paralabrax nebulifer*) captured by month in Alamitos Bay from May 1992 through November 1995 (n=435 tows). Error bars represent + one standard error for the total number of barred sand bass per 100 m^2 captured by month.

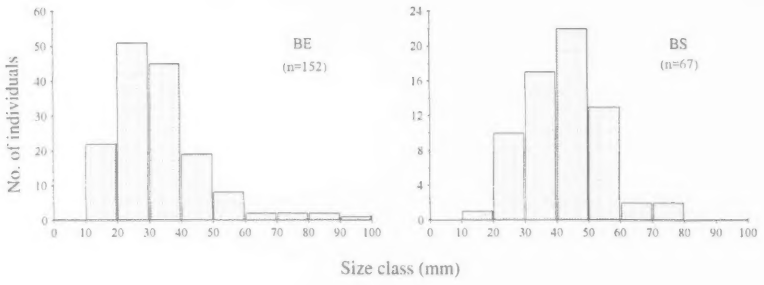


Figure 6

Length-frequency distributions of barred sand bass (*Paralabrax nebulifer*) captured in eelgrass (*Zostera marina*) habitat in Alamitos Bay from May 1992 through November 1995. See Figure 3 for further explanation.

beds. Eelgrass beds may be productive foraging areas for them. Although the diet of newly recruited and small juvenile barred sand bass is not known, larger juvenile barred sand bass (123–239 mm SL) consume amphipods, shrimps, and other small crustaceans (Roberts et al., 1984). These items are often abundant in eelgrass beds, and this plentiful food supply may enable them to achieve faster growth rates, enabling them to achieve a size that is less vulnerable to predation more quickly (Levin et al., 1997). Additionally, eelgrass may offer shelter because most newly recruited and juvenile barred sand bass have been observed around eelgrass or other structure such as mussels, rocks, or debris during SCUBA surveys (senior author's unpubl. data). Larger juveniles and adults are mostly found over sandy bottoms and among rocks (Turner et al., 1969; Feder et al.,1974) and are scarce in eelgrass beds (senior author's unpubl. data).

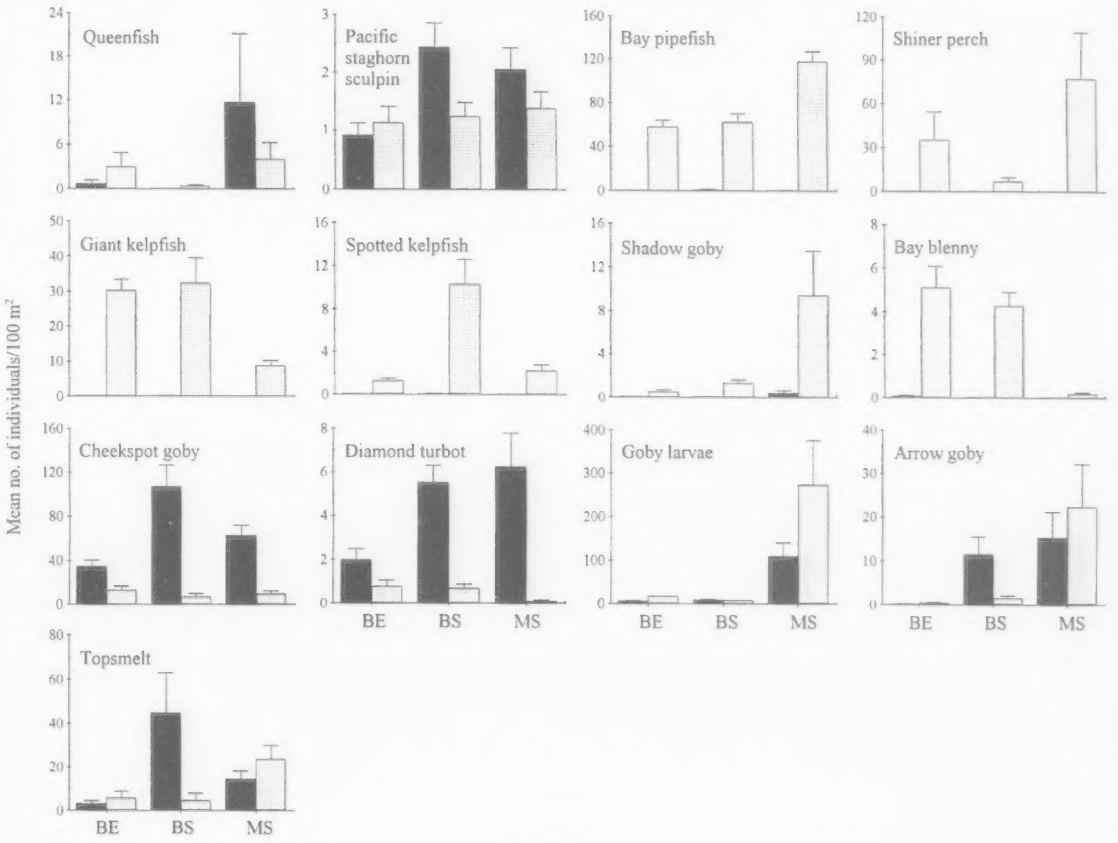


Figure 7

Mean number per 100 m² of the most abundant fishes (see text) captured in unvegetated and eelgrass (*Zostera marina*) habitats at three sites in Alamitos Bay from May 1992 through November 1995. Dark bars represent unvegetated habitats and stippled bars represent eelgrass habitats. See Figure 3 for further explanation.

The distribution patterns of California halibut and barred sand bass among sites were similar; abundances of individuals decreased with increasing distance from the bay mouth. These patterns in Alamitos Bay might be expected if abundances were related to larval supply because both species spawn outside the bay. Others have found that circulation patterns may limit dispersal of recruits to inner parts of an embayment (Sogard et al., 1987; Jenkins et al., 1996). However, this does not seem to be the case for Alamitos Bay because it is well circulated with a net inflow of water, and the distance between sites is relatively short. Instead, fewer halibut and barred sand bass may inhabit the inner parts of the bay because settlement and location of suitable habitat have occurred before reaching these areas. For California halibut, few larvae are found in embayments (White, 1977; Leithiser, 1981; Nordby, 1982; Yoklavich et al., 1992); the greatest densities of eggs and early larvae occur in nearshore waters with older larvae found less than 1 km from shore (Ahlstrom and Moser, 1975; Gruber et al., 1982; Barnett et al., 1984; Lavenberg et al., 1986; Walker et al., 1987; Moser and Watson, 1990). Most transforming halibut larvae are found on the open coast (Kramer, 1990, 1991a), and large numbers of halibut settle there and in embayments (Allen, 1988; Allen and Herbinson, 1990, 1991; Kramer, 1990, 1991a, 1991b). Those halibut that settle on the open coast move into embayments or die (Kramer, 1991a). Although it is not known where most barred sand bass recruitment occurs, spawning occurs in nearshore waters, and the planktonic larval phase is relatively short, lasting about one month (Butler et al., 1982). Therefore, if

Table 4

Results of Dunn multiple comparisons of fish abundance among sites. BE=Bay Entrance, BS=Belmont Shore, and MS=Marine Stadium. Comparisons among sites were done only for the habitat (eelgrass or unvegetated) where fishes were most abundant. * indicates which site showed a significantly greater abundance at $P<0.05$.

Common name	Scientific name	BE vs. BS	BE vs. MS	BS vs. MS
Eelgrass				
Bay pipefish	*Syngnathus leptorhynchus*		*MS	*MS
Shiner perch	*Cymatogaster aggregata*	*BE		*MS
Giant kelpfish	*Heterostichus rostratus*	*BS	*BE	*BS
Spotted kelpfish	*Gibbonsia elegans*	*BS		*BS
Shadow goby	*Quietula y-cauda*		*MS	
Bay blenny	*Hypsoblennius gentilis*		*BE	*BS
Goby larvae	Gobiidae		*MS	*MS
Unvegetated				
Cheekspot goby	*Ilypnus gilberti*	*BS	*MS	
Diamond turbot	*Hypsopsetta guttulata*	*BS	*MS	*MS
Arrow goby	*Clevelandia ios*	*BS	*MS	
Topsmelt	*Atherinops affinis*	*BS		

habitat is suitable, one would expect more newly settled California halibut and newly recruited barred sand bass at sites nearest the entrance because they are more likely to encounter these areas first. This might be especially true for embayments where the entrance is small, such as in Alamitos Bay, which could enhance chances of individuals encountering a shallow site nearest the mouth of the bay.

It is also possible that the distribution patterns we observed were due to active site selection. Diamond turbot, whose larvae also occur in nearshore waters (Barnett et al., 1984; Walker et al., 1987) and are thus exposed to the same hydrodynamic processes, were most abundant in the inner part of the bay and least abundant nearest the mouth of the bay. Kramer (1991b) also obtained opposite distribution patterns for juvenile California halibut and diamond turbot. Burke (1995) found that the distribution of two newly settled flounders that immigrated to an estuary were influenced by the availability of preferred prey types. Although we have no data on invertebrate prey distributions among sites, it is possible that California halibut and diamond turbot also select sites on the basis of availability of their preferred food items. Juvenile California halibut and diamond turbot have very different diets: small juvenile California halibut feed mainly on small crustaceans (Haaker, 1975; Plummer et al., 1983; Allèn, 1988; Drawbridge, 1990), whereas juvenile diamond turbot feed mainly on polychaetes (Lane, 1975). As halibut grow larger, they become more piscivorous and gobies become an increasingly important part of their diet (Allen, 1988; Drawbridge, 1990). This might explain why we found relatively larger halibut at Belmont Shore than at Bay Entrance because this area contained more arrow gobies and cheekspot gobies. Inhabiting an area with preferred food items might lead to accelerated growth rates, which may be an advantage for reducing size-selective predation. Sogard (1992) found that winter flounder (*Pleuronectes americanus*) and tautog (*Tautoga onitis*) were most abundant in estuarine areas that supported faster growth rates. However, we can not discount that larval supply may also be a factor because the spawning locations of diamond turbot are not known. Lane (1975) suggested that spawning takes place in or very near the outer harbor. This area would be much closer than where halibut spawn, and inner parts of the bay would be closer to eggs and larvae. In addition, laboratory experiments indicate that diamond turbot larvae are able to survive longer periods of starvation than halibut larvae (Gadomski and Petersen, 1988). This may enable diamond turbot larvae to remain in the water column longer and reach inner parts of the bay whereas halibut larvae must settle earlier.

Barred sand bass may also actively select sites within Alamitos Bay. However, the differences in physical characteristics of eelgrass among sites appeared not to affect the abundance of new recruits and juveniles. Although Bay Entrance had significantly more eelgrass shoots and longer blade lengths than Belmont Shore, barred sand bass abundances at the two sites were not significantly different. This lack of difference suggests that the effect of seagrass physical characteristics on fish abundance breaks down over larger spatial scales. However, if barred sand bass settle indiscriminately into the first eelgrass bed encountered, we would have expected significantly more individuals nearest the bay mouth. Sogard (1989)

found that initial settlement patterns for some fishes in seagrass beds were altered considerably by movement to other areas. Our results indicate that this may be also true for barred sand bass because significantly larger fish were found at Belmont Shore, indicating that movement to this site from the site nearest the entrance after initial settlement may have occurred. However, we are not able to resolve why barred sand bass were absent from the inner part of the bay.

Densities of newly settled and juvenile California halibut in our study were much greater than those reported by others using similar gear in other bays. Kramer (1990) obtained maximum monthly means for shoreline habitats in Agua Hedionda Lagoon of 3.7 newly settled California halibut per 100 m^2 for all stations combined and 9.2 per 100 m^2 for a single station. These densities are approximately 25% and 11%, respectively, of the values we obtained for Alamitos Bay. Our maximum monthly mean number of newly settled California halibut was approximately four times greater than that obtained for nearby Anaheim Bay in 1989 (Allen and Herbinson, 1990). Thus, our results support the conclusion by Allen and Herbinson (1990) that there is a great deal of annual variability in numbers of newly settled and juvenile California halibut within and among embayments in southern California.

Although the beam trawl may capture demersal fishes such as California halibut less effectively in eelgrass beds than in unvegetated areas, this seems an unlikely explanation for the great differences in habitat specific fish abundances that we observed. First, we collected large amounts of eelgrass blades (occasionally with attached rhizome) in many tows, and SCUBA observations indicated that the beam trawl maintained continuous contact with the substrate in both habitats. Second, staghorn sculpin, which rest on the substrate, and shadow goby, which often burrow in the sediment, were frequently captured in both habitats. Because we collected data only at low tides during daylight hours, we have no information on how sampling at different tide heights and times of the day would have affected our results. Diel differences in fish abundance can occur in southern California bays (Horn, 1980; Hoffman[4]); however, there are no data to suggest that these differences are related to habitats or locations within the bay.

Other species

Alamitos Bay was typical of other temperate bay-estuarine environments in having relatively few species account for a large proportion of the total number of individuals collected (reviewed in Allen and Horn, 1975; Horn, 1980; Allen, 1982; Onuf and Quammen, 1983; Allen and Herbinson, 1991; Hoffman[4]; MBC Applied Environmental Sciences[5]). Species composition and abundance were very similar to data collected using similar gear in Anaheim Bay and Agua Hedionda Lagoon (Allen and Herbinson, 1991; MBC Applied Environmental Sciences[5]). Our results, however, lacked high abundances of northern anchovy (*Engraulis mordax*), slough anchovy (*Anchoa delicatissima*), deepbody anchovy (*Anchoa compressa*), and California killifish (*Fundulus parvipinnis*) found by other studies in the inner part of Alamitos Bay and Newport Bay (Allen and Horn, 1975; Allen, 1982). Differences in sampling gear and location are probably responsible, but other factors may also play a role. As noted by Allen and Horn (1975), the abundance of northern anchovy may have been due to high periods of recruitment. Indeed, recruitment biomass of northern anchovy (age zero at 1 July) off southern California during their studies (1973 and 1979) was 2.6–3.1 times greater than during 1992–94 (Jacobson et al.[6])

For most species, greater abundances of individuals in either eelgrass or unvegetated areas suggested habitat preferences or differential mortality for these species in shallow water of Alamitos Bay. The large numbers of species and individuals in eelgrass beds indicated the importance of this habitat for many fishes, especially juveniles during spring and summer. Many of the fishes also differed in abundance across sites. More species were found near the bay mouth owing in part, to the occasional presence of more typical nearshore residents, but more individuals of several species were found farther inside the bay. However, the differences in eelgrass physical characteristics among sites did not appear to affect the abundances of most fishes. For example, abundances of bay blenny, bay pipefish, and shadow goby were not significantly different between Bay Entrance and Belmont Shore, although eelgrass density and blade lengths were significantly different between these sites. In addition, giant kelpfish and spotted kelpfish were most abundant at Belmont Shore, the site with the lowest eelgrass density and

[4] Hoffman, R. S. 1986. Fishery utilization of eelgrass (*Zostera marina*) beds and non-vegetated shallow water areas in San Diego Bay. National Marine Fisheries Service, Southwest Region, 501 W. Ocean Blvd, Suite 4200, Long Beach, CA, 90802. Admin. Rep. SWR-86-4, 29 p.

[5] MBC Applied Environmental Sciences. 1990. Distribution of juvenile California halibut (*Paralichthys californicus*) and other fishes in bay and coastal habitats of Los Angeles, Orange, and San Diego counties in 1989. MBC Applied Environmental Sciences, 947 Newhall Street, Costa Mesa, CA 92627. Final Rep. 90-RD-09, 27 p.

[6] Jacobson, L. D., N. C. H. Lo, S. F. Herrick Jr., and T. Bishop. 1995. Spawning biomass of the northern anchovy in 1995 and status of the coastal pelagic fishery during 1994. Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, P. O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-95-11, 49 p.

shortest blade lengths. Only shiner perch abundance appeared related to eelgrass physical characteristics. This was not surprising because shiner perch are closely associated with the amount of eelgrass cover (Onuf and Quammen, 1983).

In conclusion, we found that for Alamitos Bay: 1) shallow unvegetated and eelgrass habitats were important for many fishes, especially juveniles, 2) juvenile California halibut and barred sand bass used different habitats; California halibut inhabited unvegetated areas and barred sand bass inhabited eelgrass beds, 3) habitats nearest the bay mouth were particularly important for juvenile California halibut and barred sand bass, whereas habitats farther inside the bay were more important for other fishes, 4) habitat and site selection for juvenile California halibut, barred sand bass, and most other fishes appeared unrelated to physical characteristics of eelgrass or abiotic factors, 5) habitat and site selection for juvenile California halibut and barred sand bass may be related to larval supply and to the first suitable habitat and site encountered, but may be modified subsequently by movement into other areas in search of preferred food items. A closer look at shallow unvegetated and eelgrass habitats in other bays in relation to California halibut and barred sand bass abundance is warranted. Protection of these habitats from elimination or even alteration may be important for the successful management of these species.

Acknowledgments

This work was primarily funded through the Federal Aid in Sport Fish Restoration Act. We thank the following individuals for invaluable assistance in the field: Mary Larson, Paul Gregory, Kris Rager, other California Dept. of Fish and Game staff, and students from California State University at Long Beach. Calvin Chun helped with the statistical analyses. We also thank David Parker, Rick Klingbeil, Larry Allen, Calvin Chun, and three anonymous reviewers who provided valuable comments on this manuscript.

Literature cited

Adams, S. M.
1976. The ecology of eelgrass, *Zostera marina* (L.), fish communities. I. Structural analysis. J. Exp. Mar. Biol. Ecol. 22:269–291.

Ahlstrom, E. H., K. Amaoka, D. A. Hensley, H. G. Moser, and B. Y. Sumida.
1984. Pleuronectiformes:development. *In* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall Jr., and S. L. Richardson (eds.), Ontogeny and systematics of fishes, p. 640–670. Am. Soc. Ichthyol. Herpetol., Spec. Publ. 1.

Ahlstrom, E. H., and H. G. Moser.
1975. Distributional atlas of fish larvae in the California Current region: flatfishes, 1955–1960. Calif. Coop. Oceanic Fish. Invest. Atlas 23.

Allen, L. G.
1982. Seasonal abundance, composition, and productivity of the littoral fish assemblage in upper Newport Bay, California. Fish. Bull. 80:769–789.
1988. Recruitment, distribution, and feeding habits of young-of-the-year California halibut (*Paralichthys californicus*) in the vicinity of Alamitos Bay-Long Beach Harbor, California, 1983–1985. Bull. So. Calif. Acad. Sci. 87:19–30.

Allen, L. G., and M. H. Horn.
1975. Abundance, diversity, and seasonality of fishes in Colorado Lagoon, Alamitos Bay, California. Estuarine Coastal Mar. Sci. 3:371–380.

Allen, M. J., and K. T. Herbinson.
1990. Settlement of juvenile California halibut, *Paralichthys californicus*, along the coasts of Los Angeles, Orange, and San Diego Counties in 1989. Calif. Coop. Oceanic Fish. Invest. Rep. 31:84–96.
1991. Beam-trawl survey of bay and nearshore fishes of the soft-bottom habitat of southern California in 1989. Calif. Coop. Oceanic Fish. Invest. Rep. 32:112–127.

Barnett, A. M., A. E. Jahn, P. D. Sertic, and W. Watson.
1984. Distribution of ichthyoplankton off San Onofre, California, and methods for sampling very shallow coastal waters. Fish. Bull. 82:97–111.

Bell, J. D., A. S. Steffe, and M. Westoby.
1988. Location of seagrass beds in estuaries: effects on associated fish and decapods. J. Exp. Mar. Biol. Ecol. 122:127–146.

Bell, J. D., and M. Westoby.
1986a. Importance of local changes in leaf height and density to fish and decapods associated with seagrasses. J. Exp. Mar. Biol. Ecol. 104:249–274.
1986b. Variation in seagrass height and density over a wide spatial scale: effects on common fish and decapods. J. Exp. Mar. Biol. Ecol. 104:275–295.

Bell, J. D., M. Westoby, and A. S. Steffe.
1987. Fish larvae settling in seagrass: do they discriminate between beds of different leaf density? J. Exp. Mar. Biol. Ecol. 111:133–144.

Borton, S. F.
1982. A structural comparison of fish assemblages from eelgrass and sand habitats at Alki Point, Washington. M.S. thesis, Univ. Washington, Seattle, WA, 85 p.

Brothers, E. B.
1975. Comparative ecology and behavior of three sympatric gobies. Ph.D. diss., Univ. Calif., San Diego, CA, 370 p.

Burke, J. S.
1995. Role of feeding and prey distribution of summer and southern flounder in selection of estuarine nursery habitats. J. Fish Biol. 47:355–366.

Burke, J. S., J. M. Miller, and D. E. Hoss.
1991. Immigration and settlement pattern of *Paralichthys dentatus* and *P. lethostigma* in an estuarine nursery ground, North Carolina, U.S.A. Neth. J. Sea Res. 27:393–405.

Butler, J. L., H. G. Moser, G. S. Hageman, and L. E. Nordgren.
1982. Developmental stages of three California sea basses (*Paralabrax*, Pisces, Serranidae). Calif. Coop. Oceanic Fish. Invest. Rep. 23:252–268.

California Coastal Zone Conservation Commissions.
1975. California coastal plan. State Printing Office, Sacramento, CA, 443 p.

Drawbridge, M.A.
1990. Feeding relationships, feeding activity and substrate preferences of juvenile California halibut, *Paralichthys californicus*, in coastal and bay habitats. M.S. thesis, San Diego State Univ., San Diego, CA, 214 p.

Feder, H. M., C. H. Turner, and C. Limbaugh.
1974. Observations on fishes associated with kelp beds in southern California. Calif. Dep. Fish Game, Fish Bull. 160, 144 p.

Ferrell, D. J., and J. D. Bell.
1991. Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. Mar. Ecol. Prog. Ser. 72:15–24.

Frey, W. H., ed.
1971. California's living marine resources and their utilization. Calif. Dep. Fish Game, Sacramento, CA, 148 p.

Gadomski, D. M., S. M. Caddell, L. R. Abbott, and T. C. Caro.
1990. Growth and development of larval and juvenile California halibut, *Paralichthys californicus*, reared in the laboratory. *In* C. W. Haugen (ed.), The California halibut, *Paralichthys californicus*, resource and fisheries, p. 85–98. Calif. Dep. Fish Game, Fish Bull. 174.

Gadomski, D. M., and J .H. Petersen.
1988. Effects of food deprivation on larvae of two flatfishes. Mar. Ecol. Prog. Ser. 44:103–111.

Gruber, D., E. H. Ahlstrom, and M. M. Mullin.
1982. Distribution of ichthyoplankton in the Southern California Bight. Calif. Coop. Oceanic Fish. Invest. Rep. 23: 172–179.

Gunderson, D. R., and I. E. Ellis.
1986. Development of a plumb staff beam trawl for sampling demersal fauna. Fish. Res. 4:35–41.

Haaker, P. L.
1975. The biology of the California halibut, *Paralichthys californicus* (Ayres), in Anaheim Bay, California. *In* E. D. Lane and C. W. Hill (eds.), The marine resources of Anaheim Bay, p. 137–151. Calif. Dep. Fish Game, Fish Bull. 165.

Heck, K. L., Jr., K. W. Able, M. P. Fahay, and C. T. Roman.
1989. Fishes and decapod crustaceans of Cape Cod eelgrass meadows: species composition, seasonal abundance patterns and comparison with unvegetated substrates. Estuaries 12:59–65.

Heck, K. L., Jr., and T. A. Thoman.
1981. Experiments on predator-prey interactions in vegetated aquatic habitats. J. Exp. Mar. Biol. Ecol. 53:125–134.

Hollander, M., and D. A. Wolfe.
1973. Nonparametric statistical methods. John Wiley and Sons, New York, NY, 503 p.

Horn, M. H.
1980. Diel and seasonal variation in abundance and diversity of shallow-water fish populations in Morro Bay, California. Fish. Bull. 78:759–770.

Horn, M. H., and L. G. Allen.
1976. Numbers of species and faunal resemblance of marine fishes in California bays and estuaries. Bull. So. Cal. Acad. Sci. 75:159–170.

Jenkins, G. P., M. J. Wheatley, and A. G. B. Poore.
1996. Spatial variation in recruitment, growth, and feeding of postsettlement King George whiting, *Sillaginodes punctata*, associated with seagrass beds of Port Phillip Bay, Australia. Can. J. Fish. Aquat. Sci. 53:350–359.

Kramer, S. H.
1990. Distribution and abundance of juvenile California halibut, *Paralichthys californicus*, in shallow waters of San Diego County. *In* C. W. Haugen (ed.), The California halibut, *Paralichthys californicus*, resource and fisheries, p. 99–126. Calif. Dep. Fish Game, Fish Bull. 174.
1991a. Growth, mortality, and movements of juvenile California halibut, *Paralichthys californicus* in shallow coastal and bay habitats of San Diego County, California. Fish. Bull. 89:195–207.
1991b. The shallow-water flatfishes of San Diego County. Calif. Coop. Oceanic Fish. Invest. Rep. 32:128–142.

Kramer, S. H., and J. S. Sunada.
1992. California halibut. *In* W. Leet, C. M. Dewees, and C. W. Haugen (eds.), California's living marine resources and their utilization, p. 94–97. Univ. California Sea Grant Extension Program, Davis, CA.

Kuipers, B. R., B. MacCurrin, J. M. Miller, H. W. van der Veer, and J. I. J. Witte.
1992. Small trawls in juvenile flatfish research: their development and efficiency. Neth. J. Sea Res. 29:109–117.

Lane, E. D.
1975. Quantitative aspects of the life history of the diamond turbot, *Hypsopsetta guttulata* (Girard), in Anaheim Bay. *In* E. D. Lane and C. W. Hill (eds.), The marine resources of Anaheim Bay, p. 153–173. Calif. Dep. Fish Game, Fish Bull. 165.

Lavenberg, R. J., G. E. McGowan, A. E. Jahn, J. H. Petersen, and T. C. Sciarrota.
1986. Abundance of southern California nearshore ichthyoplankton: 1979–1984. Calif. Coop. Oceanic Fish. Invest. Rep. 27:53–64.

Leber, K. M.
1985. The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. Ecology 66:1951–1964.

Leithiser, R. M.
1981. Distribution and seasonal abundance of larval fishes in a pristine southern California salt marsh. Rapp. P.-V. Reuns. Cons. Int. Explor. Mer 178:174–175.

Levin, P. S.
1994. Fine-scale temporal variation in recruitment of a temperate demersal fish: the importance of settlement versus post-settlement loss. Oecologia 97:124–133.

Levin, P. S., R. Petrik, and J. Malone.
1997. Interactive effects of habitat selection, food supply and predation on recruitment of an estuarine fish. Oecologia 112:55–63.

Love, M. S., A. Brooks, and J. R. R. Ally.
1996a. An analysis of commercial passenger fishing vessel fisheries for kelp bass and barred sand bass in the Southern California Bight. Calif. Fish and Game 82:105–121.

Love, M. S., A. Brooks, D. Busatto, J. Stephens, and P. A. Gregory.
1996b. Aspects of the life histories of the kelp bass, *Paralabrax clathratus*, and barred sand bass, *P. nebulifer*, from the Southern California Bight. Fish. Bull. 94:472–481.

Moser, H. G., and W. Watson.
1990. Distribution and abundance of early life history stages of the California halibut, *Paralichthys californicus*, and comparisons with the fantail sole, *Xystreurys liolepis*. *In* C. W. Haugen (ed.), The California halibut, *Paralichthys californicus*, resource and fisheries, p. 31–84. Calif. Dep. Fish Game, Fish Bull. 174.

Nordby, C. S.
1982. The comparative ecology of ichthyoplankton within Tijuana Estuary and in adjacent nearshore waters. M.S. thesis, San Diego State Univ., San Diego, CA, 101 p.

Ono, D. S.
1992. Sand basses. *In* W. Leet, C. M. Dewees, and C. W. Haugen (eds), California's living marine resources and their utilization, p. 151–153. Univ. California Sea Grant Extension Program, Davis, CA.

Onuf, C. P., and M. L. Quammen.
1983. Fishes in a California coastal lagoon: effects of major storms on distribution and abundance. Mar. Ecol. Prog. Ser. 12:1–14.

Orth, R. J., and K. L. Heck Jr.
1980. Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay-fishes. Estuaries 3:278–288.

Orth, R. J., K. L. Heck Jr., and J. V. van Montrfans.
1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7:339–350.

Plummer, K. M., E. E. Demartini, and D. A. Roberts.
1983. The feeding habits and distribution of juvenile-small adult California halibut, (*Paralichthys californicus*) in coastal waters off northern San Diego county. Calif. Coop. Oceanic Fish. Invest. Rep. 24:194–201.

Roberts, D. A., E. E. DeMartini, and K. M. Plummer.
1984. The feeding habits of juvenile-small adult barred sand bass (*Paralabrax nebulifer*) in nearshore waters off northern San Diego County. Calif. Coop. Oceanic Fish. Invest. Rep. 25:105–111.

Rogers, S. I.
1992. Environmental factors affecting the distribution of sole (*Solea solea* (L.)) within a nursery area. Neth. J. Sea Res. 29:153–161.

Rosales-Casián, J. A.
1997. Inshore soft-bottom fishes of two coastal lagoons on the northern Pacific Coast of Baja California. Calif. Coop. Oceanic Fish. Invest. Rep. 38:180–192.

Sogard, S. M.
1989. Colonization of artificial seagrass by fishes and decapod crustaceans: importance of proximity to natural eelgrass. J. Exp. Mar. Biol. Ecol. 133:15–37.
1992. Variability in growth rates of juvenile fishes in different estuarine habitats. Mar. Ecol. Prog. Ser. 85:35–53.

Sogard, S. M., and K. W. Able.
1991. A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitat for epibenthic fishes and decapods. Estuarine Coastal Shelf Sci. 33:501–519.

Sogard, S. M., and B. L. Olla.
1993. The influence of predator presence on utilization of artificial seagrass habitats by juvenile walleye pollock, *Theragra chalcogramma*. Environ. Biol. Fishes 37:57–65.

Sogard, S. M., G. V. N. Powell, and J. G. Holmquist.
1987. Epibenthic fish communities on Florida Bay banks: relations with physical parameters and seagrass cover. Mar. Ecol. Prog. Ser. 40:25–39.

Tanda, M.
1990. Studies on burying ability in sand and selection to the grain size for hatchery-reared marbled sole and Japanese flounder. Nippon Suisan Gakkaishi 56(10): 1543–1548.

Turner, C. H., E. E. Ebert, and R. R. Given.
1969. Man Made Reef Ecology. Calif. Dep. Fish Game, Fish Bull. 146, 221 p.

Underwood, A. J.
1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. Mar. Biol. Ann. Rev. 19:513–605.

Walker, H. J. Jr., W. Watson, and A. M. Barnett.
1987. Seasonal occurrence of larval fishes in the nearshore Southern California Bight off San Onofre, California. Estuarine Coastal Shelf Sci. 25:91–109.

White, W. S.
1977. Taxonomic composition, abundance, distribution and seasonality of fish eggs and larvae in Newport Bay, California. M.A. thesis, Calif. State Univ., Fullerton, Fullerton, CA, 107 p.

Worthington, D. G., D. J. Ferrell, S. E. McNeill, and J. D. Bell.
1992. Effects of shoot density of seagrass on fish and decapods: are correlation evident over larger spatial scales? Mar. Biol. 112:139–146.

Yoklavich, M. M., M. Stevenson, and G. M. Cailliet.
1992. Seasonal and spatial patterns of ichthyoplankton abundance in Elkhorn Slough, California. Estuarine Coastal Shelf Sci. 34:109–126.

Zar, J. H.
1984. Biostatistical analysis. Prentice-Hall, Inc., Englefield Cliffs, NJ, 718 p.

Movements of haddock, *Melanogrammus aeglefinus*, on eastern Georges Bank determined from a population model incorporating temporal and spatial detail

Lutgarde A.M. Van Eeckhaute

Stratis Gavaris

Edward A. Trippel

Biological Station
Department of Fisheries and Oceans
St. Andrews, New Brunswick E0G 2X0, Canada
E-mail address (for L. A. M. Van Eeckhaute): Van-EeckhauteL@mar.dfo-mpo.gc.ca

Abstract.—A population model incorporating temporal and spatial detail revealed that the majority of eastern Georges Bank haddock, *Melanogrammus aeglefinus*, were found on the Canadian side of the Canada-U.S. boundary. During spring they were more widespread across the top of the bank and subsequently migrated eastward so that by fall almost all haddock were found in the deeper waters on the Canadian side. There is a return migration to the top of the bank during the winter. The seasonal distribution and migration of haddock has remained stable since 1985 and migration rates do not appear to be related to the observed range of abundance. The distribution pattern since 1985 appears similar to that observed between 1972 and 1984. In contrast, during 1963–71 haddock were more widespread throughout the area in both spring and fall. Abundance of haddock in the Georges Bank and Gulf of Maine area was exceptionally high in the earlier period, and haddock from the spawning component in the Great South Channel area may have accounted for a greater augmentation to the eastern Georges Bank population. In implementing strategies for managing this transboundary resource, scientists will need to evaluate the nature of haddock distributions in order, in turn, to evaluate the implications of their strategies.

Manuscript accepted 25 June 1998.
Fish. Bull. 97:661–679 (1999).

The haddock, *Melanogrammus aeglefinus*, on Georges Bank have supported a commercial fishery since the early 1900s. Since 1977, with the extension of jurisdiction by coastal states, only Canada and the United States have conducted haddock fisheries on Georges Bank. In October 1984 the International Court of Justice (ICJ) established a maritime boundary between Canada and the United States in the Gulf of Maine area. Subsequently, fishing by Canada and the United States on Georges Bank has been restricted to these respective jurisdictions (Fig. 1). The new boundary line, referred to as the ICJ line in our study, lies over an established grid of statistical unit areas that has been used to summarize landings data since the 1930s. These areas have been based on, among other factors, considerations of biological stock structure (principally cod, *Gadus morhua*, and haddock), political boundaries, and practicalities of data collection (Halliday and Pinhorn, 1990). Aggregates of unit areas are used to determine the boundaries of fisheries "management units"—geographic areas defined for regulatory purposes.

Prior to establishment of the maritime boundary, regulation of the haddock fishery was based on a management unit encompassing all of subarea 5, although it was recognized that this unit included at least two major spawning concentrations (Walford, 1938; Bigelow and Schroeder, 1953). Historical evidence indicates that the most important spawning concentration was on the eastern part of Georges Bank whereas the spawning was variable among years over the Great South Channel and the southern part of the bank (Walford, 1938). Tagging studies and other biological data have shown that little mixing occurs between haddock on Georges Bank and those in surrounding areas, e.g. 4X (Fig. 1), which is situated north and east of Georges Bank (Schuck and Arnold, 1951; Grosslein, 1962; Clark et al., 1982). Tagging studies have also indicated limited east–west movement within subdivision 5Ze, which is the eastern portion of division 5Z and includes unit areas g, h, j, m, n, and o (Fig. 1), as only about 5% of returns from haddock tagged off Cape Cod were reported from areas east of 68°W and 95% of returns from haddock tagged on eastern Georges Bank were reported from areas east of 69°W (Grosslein, 1962). In 1990, Canada adopted unit areas 5Zj and 5Zm,

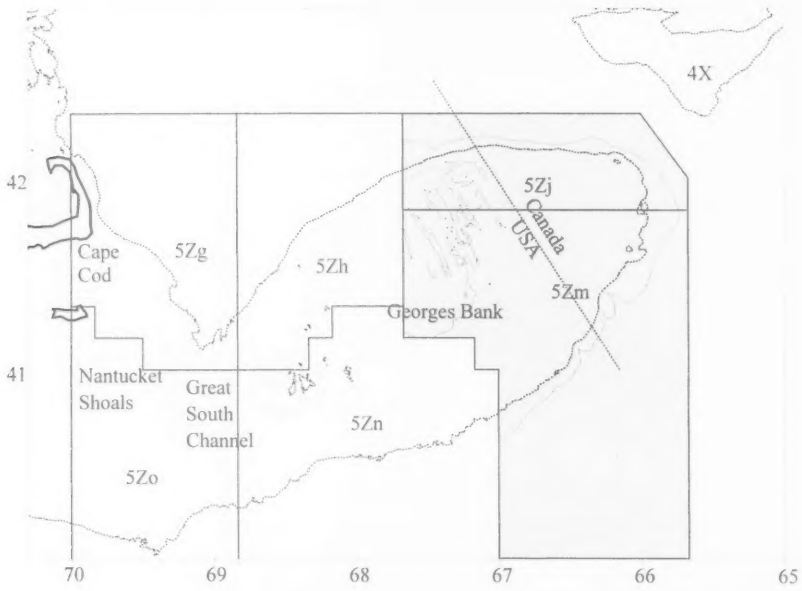


Figure 1

Fisheries statistical unit areas in NAFO subdivision 5Ze (includes 5Zg,h,j,m,n,o). The Canadian management unit for haddock comprises unit areas 5Zj and 5Zm (shaded).

eastern Georges Bank, as a management unit. Gavaris and Van Eeckhaute (1990) summarized the considerations on which the management unit boundaries are based. The ICJ line bisects this management unit and imposes additional complexity for resource management considerations in the absence of consistent practices by the two jurisdictions. A prerequisite to investigation of harvest strategies for the transboundary haddock resource is an understanding of haddock distribution and migration on eastern Georges Bank in relation to the ICJ line.

Earlier studies have described spatial distribution of Georges Bank haddock and patterns in relation to season, topography, time, and hydrographic conditions (Colton, 1955; Grosslein, 1962; Overholtz, 1985, 1987). Our study focuses on the relative distribution and net migration rates of haddock within the 5Zj,m Canadian management unit in relation to the ICJ line. Our objectives were to describe the relative abundance of haddock on the Canadian and U.S. sides of eastern Georges Bank since 1963 and to estimate rates of migration for haddock across the ICJ line since 1985 when fishery statistics first became available at a resolution sufficient to be summarized with respect to the ICJ line. These results are necessary for the evaluation of the effects of regulatory measures, whether unilateral or bilateral.

Methods

Relative abundance

Results from research vessel bottom trawl surveys were used to estimate haddock abundance on the Canadian and U.S. sides of the ICJ line on eastern Georges Bank and to subsequently derive ratios of abundance on the Canadian side to total 5Zj,m abundance. Annual surveys have been conducted by the U.S. National Marine Fisheries Service (NMFS) during the fall since 1963 and during the spring since 1968 and by the Canadian Department of Fisheries and Oceans (DFO) during the spring since 1986. Ratios of relative abundance were calculated to 1993 for the NMFS surveys and to 1994 for the DFO surveys, but survey data beyond those years were used to illustrate haddock distribution patterns as the data became available. All surveys used a stratified random design but the strata boundaries differed (Fig. 2). The strata boundaries for the DFO survey were modified to incorporate the ICJ line as a border in 1987. The results from the DFO survey in 1986, which used a different strata design, were not considered in our study owing to the complication that such a design would introduce and to the limited additional information that would result.

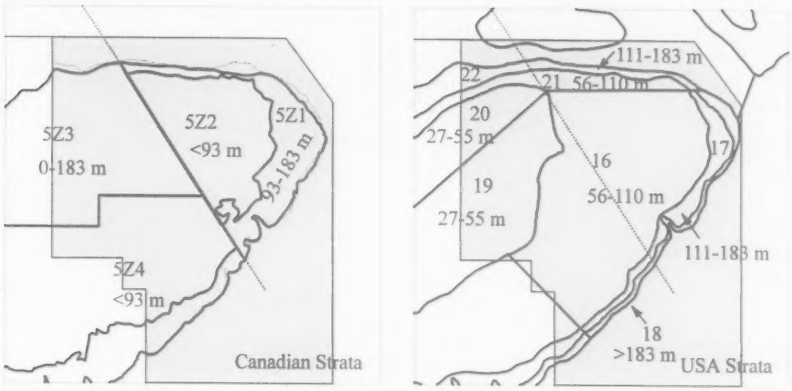


Figure 2

Strata for DFO and NMFS bottom trawl surveys with depth ranges. Several NMFS strata are bisected by the Canada-U.S. boundary line. Some strata for both countries are bisected by the 5Zj and 5Zm unit area boundaries.

The DFO surveys have been conducted by the RV *Alfred Needler* and for one year, by its sister ship, the RV *Wilfred Templeman*, with a Western IIA trawl. The NMFS surveys have been conducted by the RV *Albatross IV* and the RV *Delaware II* with a BMV door until 1984 and a polyvalent door subsequently. A further gear alteration occurred with the replacement of the standard Yankee 36 trawl by a modified Yankee 41 trawl during the spring surveys in 1973–81 (Hayes and Buxton[1]). Conversion factors to account for these differences were not considered in this study because the analysis involved only within-year comparisons. In the autumn of 1985, 1986, and 1988, both NMFS vessels made tows in the 5Zjm area but there was only one instance out of the three years, 1988, which would have resulted in slightly different ratios. The boat conversion factor was therefore not applied in our study.

Abundance of haddock on each side of the ICJ line was obtained by summing the estimates of abundance for the strata in the respective jurisdictions. This method can be applied directly to the Canadian side for the DFO survey results because the strata boundaries incorporate the ICJ line; however, the strata on the U.S. side, 5Z3 and 5Z4, are bisected by the 5Zj,m unit area lines (Fig. 2). Several strata in the NMFS surveys are bisected by the ICJ line or the 5Zj,m unit area lines, or by both (Fig. 2). We refer to the parts of the bisected strata as strata sections. Because the tow locations were selected at random, we computed the abundance of haddock in the strata sections in the same manner as was done for entire strata according to the method in Smith (1988). Total abundance on either side of the ICJ line was then obtained by summing the respective abundances from strata or strata sections, or from both. Abundance for each stratum or stratum section was obtained as the average catch per tow for tows within it multiplied by the number of possible tow units within it, thereby weighting the average catch per stratum or stratum section by its area.

This approach could be applied in most instances; however, there were cases in the NMFS surveys where no tows were made in a stratum section (Tables 1 and 2). Missing observations were handled in three ways; by estimation using the multiplicative model, by assumption of a zero value, or by assigning the mean per tow obtained for the whole stratum. The multiplicative model (Gavaris, 1980) was the preferred method but it requires a ln transformation of the catch per tow from the surveys which precludes the use of "0" values in the model; therefore, for strata sections with low abundance, this model was inappropriate. The U.S. sections of strata 17 and 18 in both spring and fall surveys, the U.S. section of stratum 19 in the fall, and the Canadian section of stratum 18 in the spring had a predominance of "0" values, suggesting that it would be reasonable to assume a zero value for missing observations in those strata sections. Missing observations for U.S. stratum section 20 within 5Zj,m were assumed to be equal to the mean catch per tow obtained for the entire stratum that extends west of 5Zjm, and the age composition for the whole stratum was extrapolated to that portion lying within 5Zj,m. This procedure was first followed for the 1991 eastern Georges

[1] Hayes, D., and N. Buxton. 1992 Assessment of the Georges Bank haddock stock in 1991. Northeast Fisheries Science Center, Res. Doc. SAW 13/1. [Appendix to CRD-92-02.]

Table 1

Estimated abundance (numbers in thousands) of haddock by stratum on the Canadian and U.S. side of the ICJ line in unit areas 5Zj and 5Zm (eastern Georges Bank) from fall NMFS bottom trawl surveys. When a stratum section was not sampled, as indicated by "( )", a multiplicative model was used to estimate abundance except for the U.S. side of strata 17, 18, and 19 which were assigned an abundance of "0" and stratum 20 where the mean for the whole stratum was used. The last two columns show the percentage of the total abundance that came from nonsampled strata or strata sections, or from both.

	Stratum												Total abundance		% from non sampled	
	16		17		18		19	20	21		22					
Year	Can.	U.S.	Can.	U.S.	Can.	U.S.	U.S.	U.S.	Can.	U.S.	Can.	U.S.	Can.	U.S.	Can.	U.S.
1963	38,652	32,353	2148	0	(12,942)	0	30,950	4313	16,462	1942	(21,761)	3772	91,964	73,330	38	0
1964	31,485	45,050	667	62	358	0	45,126	8627	2095	(627)	(4535)	(555)	39,140	100,048	12	1
1965	11,434	7102	914	(0)	198	0	16,341	1849	2091	113	923	126	15,560	25,530	0	0
1966	7999	574	123	16	57	0	7034	3817	204	8	137	175	8521	11,624	0	0
1967	3543	344	131	0	102	5	1118	154	105	(50)	137	(45)	4018	1716	0	6
1968	4831	0	97	0	119	(0)	0	34	0	8	156	(16)	5203	58	0	27
1969	387	168	87	0	21	(0)	325	548	21	(12)	50	0	566	1052	0	1
1970	483	47	392	19	128	(0)	5005	0	242	8	125	(31)	1369	5111	0	1
1971	451	836	319	0	13	0	758	0	32	315	87	(39)	902	1948	0	2
1972	2313	3300	312	(0)	13	0	0	0	189	8	(375)	11	3202	3319	12	0
1973	11,515	230	735	0	19	0	0	0	347	(71)	(511)	(63)	13,128	363	4	37
1974	387	72	58	0	13	0	0	(0)	284	8	0	66	742	145	0	0
1975	6212	9756	602	(0)	64	0	108	5512	21	(92)	175	(81)	7073	15,549	0	1
1976	58,353	143	580	0	102	0	0	(0)	11,452	(236)	(1708)	55	72,195	435	2	54
1977	2641	42	421	0	(789)	0	22	0	13,809	129	1614	(162)	19,275	355	4	46
1978	6035	2374	4571	0	543	0	3809	126	821	0	271	55	12,240	6364	0	0
1979	7173	451	416	8	1465	0	22	9	491	(362)	6595	448	16,140	1299	0	28
1980	1643	112	3727	0	192	0	433	154	453	1200	1143	55	7157	1954	0	0
1981	3704	1865	1558	210	172	0	81	23	274	(180)	648	66	6356	2425	0	7
1982	591	36	1228	(0)	511	0	0	17	21	(29)	6	33	2358	115	0	25
1983	1369	947	735	(0)	192	0	0	0	158	(104)	(749)	77	3202	1127	23	9
1984	414	0	2133	(0)	141	0	0	0	116	(43)	(311)	55	3114	98	10	44
1985	5315	7231	588	(0)	324	0	0	0	568	(139)	25	(123)	6819	7493	0	3
1986	6845	0	892	(0)	358	0	0	0	2274	40	12	0	10,381	40	0	0
1987	81	179	271	(0)	115	0	135	103	316	0	312	0	1094	417	0	0
1988	2537	143	493	(0)	741	0	0	0	1179	(78)	362	0	5311	222	0	35
1989	852	47	1190	(0)	(311)	5	0	103	1379	16	573	16	4447	176	7	0
1990	564	915	1204	0	345	(0)	0	0	1165	(120)	170	(106)	3448	1141	0	20
1991	483	245	609	(0)	(124)	0	(0)	0	0	315	274	0	1491	560	8	0
1992	709	2869	1219	50	64	(0)	0	228	147	0	75	(39)	2214	3188	0	1
1993	1519	0	667	(0)	0	(0)	0	34	8041	(35)	162	(31)	10,390	99	0	66

Bank haddock assessment (Gavaris and Van Eeckhaute, 1991) and therefore the method used then was followed in our study. For all other missing observations that occurred in strata which did not have a predominance of zero values, a multiplicative model employing strata and years as factors influencing the mean catch per tow was used to derive predicted values:

$$\ln I_{s,y} = \ln I'_{s'y'} \sum_{s} (\ln P_s) X_s + \sum_{y} (\ln P_y) X_y + \varepsilon_{s,y},$$

where s = stratum;
y = year;
I = survey catch/tow;
P = relative power for stratum or year;
X = dummy variables indicating the stratum and year of observation; and
ε = independent identically distributed normal error.

Strata sections 17u, 18c, and 18u in the spring and strata sections 17u, 18u, and 19 in the fall were not included in the multiplicative model analysis because of the prevalence of zeros in these strata sections.

Table 2

Estimated abundance (numbers in thousands) of haddock by stratum on the Canadian and U.S. sides of the ICJ line in unit areas 5Zj and 5Zm (eastern Georges Bank) from spring NMFS bottom trawl surveys. When a strata section was not sampled, as indicated by "()", a multiplicative model was used to estimate abundance except for stratum 18 and the U.S. side of stratum 17 which were assigned an abundance of "0" and stratum 20 where the mean for the whole stratum was used. The last two columns show the percentage of the total abundance which came from nonsampled strata or strata sections, or from both.

	Stratum												Total abundance		% from non sampled	
	16		17		18		19	20	21		22					
Year	Can.	U.S.	Can.	U.S.	Can.	U.S.	U.S.	U.S.	Can.	U.S.	Can.	U.S.	Can.	U.S.	Can.	U.S.
1968	3318	1506	595	(0)	43	0	1515	274	32	(55)	(200)	77	4186	3427	5	2
1969	2164	1119	445	0	0	0	397	34	11	(25)	87	(21)	2707	1596	0	3
1970	713	7221	218	0	0	0	252	(21)	21	(26)	75	(21)	1027	7540	0	1
1971	139	430	194	0	0	5	271	0	14	73	374	(19)	720	797	0	2
1972	1002	215	310	0	0	0	144	0	91	1534	0	(20)	1403	1913	0	1
1973	2462	1052	443	(0)	0	0	685	46	21	186	1322	0	4248	1968	0	0
1974	9582	0	116	0	4	0	2841	0	416	(19)	(70)	0	10,189	2860	1	1
1975	4134	538	65	(0)	0	(0)	577	0	42	16	12	(17)	4254	1148	0	2
1976	3818	1052	629	(0)	0	(0)	406	(154)	358	16	(128)	0	4933	1628	3	9
1977	3221	502	48	0	0	0	681	1061	13,115	16	0	5	16,384	2266	0	0
1978	5738	2905	48	8	6	0	606	0	4652	(60)	33	(50)	10,479	3629	0	3
1979	7043	6743	319	23	0	(0)	401	(28)	253	0	594	87	8209	7284	0	0
1980	6120	27,212	254	54	6	(0)	24,863	(1124)	3694	0	112	(114)	10,187	53,367	0	2
1981	14,387	8704	638	3	(0)	(0)	6125	2659	1905	(246)	87	230	17,017	17,967	0	1
1982	5411	3945	416	233	6	0	397	251	1179	(113)	898	22	7910	4962	0	2
1983	1933	538	735	39	0	0	0	171	(1119)	16	87	109	3874	874	29	0
1984	2623	1255	305	(0)	0	0	433	17	105	8	37	33	3071	1746	0	0
1985	9133	574	252	31	38	0	108	0	1937	(50)	87	(41)	11,447	804	0	11
1986	6313	1521	29	0	0	0	433	0	1305	4	0	(18)	7647	1975	0	1
1987	5991	115	136	0	6	0	0	1872	126	(11)	25	(9)	6284	2007	0	1
1988	1417	1894	15	0	0	(0)	54	0	284	0	0	0	1716	1948	0	0
1989	4168	5022	392	93	153	(0)	27	0	1631	0	798	(40)	7142	5182	0	1
1990	4268	9756	44	0	(0)	(0)	0	0	1291	16	12	(23)	5615	9795	0	0
1991	9341	2254	48	(0)	0	(0)	0	0	74	0	0	0	9463	2254	0	0
1992	966	369	165	(0)	0	(0)	65	11	379	(10)	0	(8)	1510	464	0	4
1993	2791	841	551	(0)	0	(0)	0	0	365	(30)	237	(25)	3944	896	0	6

Treatment of missing observations is summarized in Table 3.

The multiplicative model requires a ln transformation of the catch per tow from the surveys. This necessitated some treatment of remaining "0" values in the data. To reduce the influence of "0" values, the strata means rather than individual tow data were used because there are frequent occurrences of "0" catch in the individual tow data. Consequently, a test for the significance of interaction between years and strata was not possible. Because a logarithmic transformation of the mean catch per tow is required, a constant less than the minimum catch was added to "0" values. To examine the impact of adding a constant to the zero observations, analyses using three different constants, 0.1, 0.01, and 0.001, were considered. It was found that smaller constants exerted a greater influence on the model's output as seen by increases in Cook's D statistic (Cook, 1977). Moreover, the frequency distribution of the residuals showed greater departure from a normal distribution when 0.01 was added and particularly when 0.001 was added, displaying a marked skew toward negative values. Consequently, 0.1 was added to zero values for multiplicative model computations. The smallest observed value greater than "0" was 0.2.

For each survey, an age-length key combining all strata on eastern Georges Bank was applied to the length composition in each stratum or stratum section to derive the age structure. The age structures to which the estimated mean number per tow for missing values were applied were taken from the

Table 3

Treatment of missing observations in the NMFS spring and fall surveys to estimate abundance on the U.S. side and the Canadian side of unit areas 5Zj and 5Zm. c = Canadian side of stratum; u = U.S. side of stratum; *M* and **M** = used in multiplicative model; **M** = missing observations estimated from multiplicative model; 5Z = 5Z stratum mean used to fill in missing observations; 0 = missing observations assigned a value of 0.

Stratum	Spring	Fall
16c	*M*	*M*
16u	*M*	*M*
17c	*M*	*M*
17u	0	0
18c	0	**M**
18u	0	0
19	*M*	0
20	5Z	5Z
21c	**M**	**M**
21u	**M**	**M**
22c	**M**	**M**
22u	**M**	**M**

adjacent stratum section of the same stratum. When both strata sections of a stratum had missing observations, the age composition from an adjacent stratum was used. Haddock abundance at age on the Canadian and U.S. sides of the ICJ line were obtained by applying the age compositions of strata and strata sections to their respective total abundance and then summing the results within each jurisdiction. A ratio of relative abundance for the Canadian side was calculated by dividing the estimate on the Canadian side by the sum of the estimates on Canadian and U.S. sides.

Instantaneous rates of net migration

The availability of fisheries statistics, since 1985, at a resolution sufficient to be summarized with respect to the ICJ line, in conjunction with the relative abundance information described above, made it possible to derive estimates of net migration rates. Catch-at-age by quarter which was required for this analysis is reported in Gavaris and Van Eeckhaute (1997).

Net migration rates were estimated by using a model that follows from one originally proposed by Beverton and Holt (1957). Terminal population abundance for each cohort at the beginning of 1994 for the 1986 to 1993 year classes and at age 8 for the 1968 to 1985 year classes was taken from Gavaris and Van Eeckhaute (1994). Population abundance in all of 5Zj,m at time y, expressed in units of years, e.g. 1991.75, for ages 1–8, a, was calculated by using virtual population analysis with a three-month time period, i.e. t=0.25, according to the following algorithm. The annual instantaneous natural mortality rate, M, was assumed constant and equal to 0.2. In all equations N refers to numbers of fish and, if preceded by a subscript letter, indicates the source of the loss so that ${}_{F}N$ is the number dying from fishing, ${}_{M}N$ is the number dying from natural mortality, and ${}_{E}N$ is the number lost or gained from migration. If not preceded by a subscript, N refers to population abundance. The method assumes an exponential decay model:

$$N_{y,a} = N_{y+t,a+t} e^{(F_{y,a}+M)t},$$

where the fishing mortality, $F_{y,a}$, for ages 1 to 7 is obtained by solving the catch equation using a Newton-Raphson algorithm with the three-month commercial catch-at-age data, ${}_{F}N_{y,a}$.

$$N_{y,a} = \frac{{}_{F}N_{y,a}(F_{y,a}+M)t}{F_{y,a}t\left(1-e^{-(F_{y,a}+M)t}\right)}.$$

The total number of fish dying due to natural mortality in each quarterly period, y, was obtained by applying the quarterly rate of natural mortality to the average population abundance during the period:

$${}_{M}N_{y,a} = Mt\overline{N},$$

where $\overline{N}$, the average population abundance during the period, is defined as

$$\overline{N}_{y,a} = \frac{N_{y,a}\left(1-e^{-(F_{y,a}+M)t}\right)}{(F_{y,a}+M)t}.$$

DFO surveys were conducted between 10 February and 19 March, whereas NMFS spring surveys were conducted from 23 March to 26 April. The NMFS fall surveys were conducted between 3 October and 25 October. The distributions of haddock obtained from the spring and fall survey results were considered to be representative of 1 April and 1 October, respectively. For each year, six-month net migration rates were calculated for the spring–summer period (1 April–30 September) and the fall–winter period (1 October–31 March).

Since proportions of haddock on the Canadian side of the ICJ line, as indicated from DFO and NMFS survey results, were available for only two points in time, spring and fall, subsequent calculations were done on a half-year basis to coincide with the survey

timing. The 5Zj,m population numbers at the beginning of quarters 2 and 4 as obtained from the quarterly VPA were used. Numbers of haddock dying from natural mortality and from fishing were summed for quarters 2 and 3 to give 1 April numbers and for quarters 4 and 1 to give 1 October numbers. The proportions of haddock at ages 1 to 8 on the Canadian side of the ICJ line were averaged for the two spring surveys for 1987 to 1993. These were then combined with the 1985 and 1986 proportions from the NMFS spring survey and, along with the NMFS fall proportions, were applied to the 5Zj,m population abundance at the beginning of quarters 2 and 4 to obtain population abundance on the Canadian side:

$$N_{Can,y,a} = N_{y,a} R_{Can,y,a},$$

where $R_{Can,y,a}$ = the proportion occurring on the Canadian side.

The number of fish dying from natural mortality on the Canadian side of the ICJ line was assumed proportional to the fraction of the population occupying the Canadian side on average during the period:

$${}_M N_{Can,y,a} = \frac{{}_M N_{y,a} \overline{N}_{Can,y,a}}{(\overline{N}_{Can,y,a} + \overline{N}_{USA,y,a})},$$

where $\overline{N}_{Can,y,a}$ and $\overline{N}_{USA,y,a}$ = the average population abundances on the Canadian and USA sides, respectively, during the period.

The net number of fish migrating from the Canadian side to the U.S. side of the ICJ line was obtained by subtracting the number of fish caught by the Canadian fishery at age, ${}^F N_{Can,y,a}$, and the number of fish dying from natural mortality on the Canadian side from the difference between population abundance on the Canadian side at the beginning of the two six month periods:

$${}_E N_{y,a} = N_{Can,y,a} - N_{Can,y+t,a+t} - {}_F N_{Can,y,a} - {}_M N_{Can,y,a}.$$

Instantaneous rates of migration were calculated in relation to the average abundance in 5Zj,m as follows:

$$E_{y,a} = \frac{{}_E N_{y,a}(Z_{y,a})}{N_{y,a}\left(1 - e^{-(Z_{y,a})}\right)},$$

where the total mortality

$$Z_{y,a} = -\ln \frac{N_{y+t,a+t}}{N_{y,a}}.$$

By convention, ${}_E N_{y,a}$ and $E_{y,a}$ is positive when the net direction of migration is towards the U.S. side and negative when it is towards the Canadian side.

Results

Ratios of relative abundance

Although the ICJ line was not established until October 1984, to provide a historical perspective of haddock relative abundance with respect to the line, we make reference to Canadian and U.S. sides of eastern Georges Bank for all surveys conducted since 1963. Because relative abundances of older haddock, greater than age 8, are difficult to interpret because of the small numbers caught, an aggregated age grouping of 9+ was used.

Fall season The multiplicative model accounted for about half of the total variation in catch per tow (multiple R^2=0.47). The stratum influence with an F-value of 7.245 and P<0.001 accounted for most of the variation, but the year effect also accounted for some with an F-value of 3.247 and P<0.001. The frequency distribution of residuals approximated a normal distribution. The strata coefficients from the multiplicative model give an indication of the relative abundances between strata sections, i.e. the higher the value, the higher the abundance. For those strata sections that were used in the model, the shading in Figure 3 was scaled to the magnitude of the strata coefficients. All Canadian sections of strata had higher coefficients than the corresponding U.S. sections. The four sections on the U.S. side that were not used in the model were dominated by zero catch per tow. Canadian strata sections having depth zones of 56 to 183 m exhibited the highest coefficients. The model results indicate that the strata on the Canadian side had higher abundance than those on the U.S. side.

For each stratum the abundances by stratum or stratum section are contained in Table 1. The dominant strata were 16c, 16u, and 17c. Abundance in 19u and 20u used to be quite high but in recent times almost no haddock have been caught there. In contrast, 17c has shown an increase in its relative abundance in recent years in comparison to early catches, although that abundance since the 1960s has dropped substantially. Total fall abundance showed that more haddock were caught on the U.S. side during the 1960s and early 1970s, after which haddock became more abundant on the Canadian side. Numbers estimated by the multiplicative model accounted for a significant amount of the abundance on the U.S. side

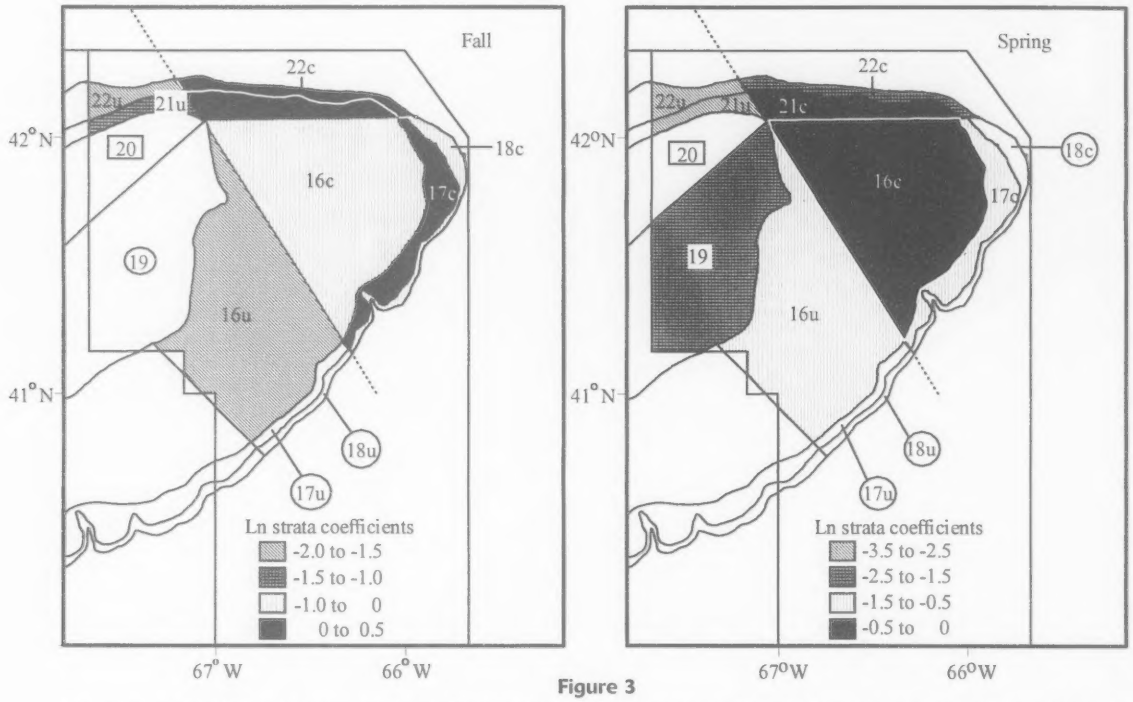


Figure 3

The relative abundances between strata as characterized by the ln strata coefficients from the multiplicative model for the NMFS fall and spring surveys. Strata which have a circle ( ) around them, e.g. 17u , were not used in the multiplicative model and missing observations were given a value of "0." Stratum 20 was also not used in the model because the 5Z stratum means were used for missing observations. Strata depth zones are as follows: 19 and 20, 27–55 m; 16 and 21, 56–110 m; 17 and 22, 111–183 m; 18, >183 m.

in several years but, in those years, the total abundance on the U.S. side was usually small. For the Canadian side, in most instances, very little of the abundance was estimated from the multiplicative model.

An examination of the fall ratios of relative abundance, (Fig. 4), revealed two distribution patterns in haddock age 1 and older. Between 1963 and 1972, haddock were highly variable in their relative abundance and were found throughout the bank. After 1971, the majority of haddock ages 1 and older were found on the Canadian side as indicated by the predominance of ratios ≥0.75. The ratios of relative abundance indicated that age-0 haddock were very variable throughout 1963–93 and were often more abundant on the U.S. side.

Friedman's nonparametric test revealed that the ratios for ages 1–9+ during the period 1972–93 were similar but the ratios for age 0 differed from these. During the period 1963–71, the ratios for all ages, 0–9+, did not show persistent patterns (Table 4).

We conclude then that the relative abundance of age-0 haddock across the ICJ line is different from that for ages 1–9+ but only during the period 1972–93. Therefore, for further analysis of time trends, ages 1–9+ were combined (Fig. 5). From 1963 to 1971 haddock of ages 1+ were distributed throughout 5Zj,m but were generally found in greater numbers on the U.S. side. Since 1972, however, very few haddock at these ages have been found on the U.S. side. Between 1963 and 1971, there was one anomolously high value, 1968 with a ratio of 0.99, but all other ratios were lower than any of the values after 1971. In contrast to ages 1+, the ratios of relative abundance of age-0 haddock were very variable and indicated a less patterned distribution, being distributed throughout 5Zj,m. All except one of the stronger year classes, 1972, 1975, 1978, 1983, 1985, 1987, and 1992, with relative abundance ratios at age 0 of 0.34, 0.28, 0.47, 0.62, 0.40, 0.21, and 0.08, respectively, were more abundant on the U.S. side. Interestingly, the weak year classes that followed these (1973, 1976, 1979, 1984, 1986, 1988, and 1993) were found in greater abundance on the Canadian side with ratios of 0.85, 0.85, 0.64, 1.0, 1.0, 1.0, and 0.93, respectively. A likely mechanism has not been determined.

The distribution of age-1+ haddock determined by using the catch-per-tow data from the NMFS fall survey, pooled over 1985–95, are shown in Figure 6. As

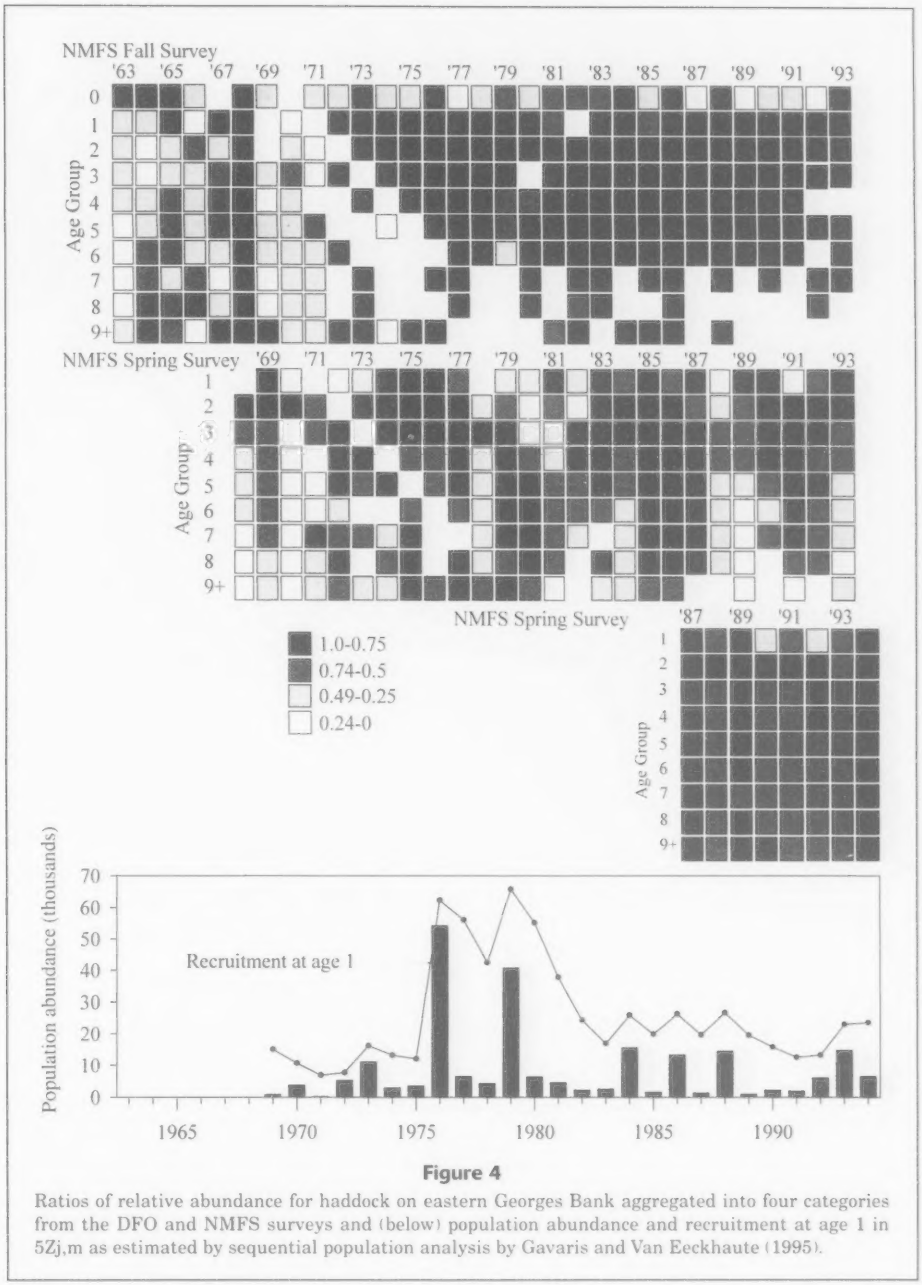


Figure 4

Ratios of relative abundance for haddock on eastern Georges Bank aggregated into four categories from the DFO and NMFS surveys and (below) population abundance and recruitment at age 1 in 5Zj,m as estimated by sequential population analysis by Gavaris and Van Eeckhaute (1995).

noted from the analyses of ratios of relative abundance, in recent times few haddock have been found on the U.S. side during the fall. For comparison purposes the 1963–71 distribution determined by using NMFS fall survey data are also shown. It is evident that the 1963–71 distribution pattern is markedly different from the 1985–95 patterns. The wide spread abundance observed west of the ICJ line in the 1963–71 period is no longer present in recent times and the aggregations on the northeast peak that were apparent from 1985 to 1995 were not evident in the earlier period.

Spring season As with the fall results, the multiplicative model accounted for about half of the total

Table 4

Probability estimates of Freidmans's nonparametric test for randomness within ages from the National Marine Fisheries Service (NMFS) and Canadian Department of Fisheries and Oceans (DFO) survey ratios of relative abundance for two age groupings.

Age groups	Years	*F*-value	Degrees of freedom	Probability of test criterion
NMFS fall sSurvey				
0–9+	1963–71	8.424	9	$0.5 > P > 0.25$
0–9+	1972–93	25.185	9	$0.005 > P > 0.001$
1–9+	1972–93	0.8	8	$P > 0.999$
NMFS spring survey				
1–9+	1968–93	28.292	8	$0.001 > P$
DFO spring survey				
1–9+	1987–94	6.058	8	$0.75 > P > 0.5$

variation in catch per tow (multiple R^2=0.41). The stratum influence accounted for most of the variation with an *F*-value of 8.389 and $P<0.001$ but the year effect was not as strong for the spring survey as it was for fall (*F*-value of 1.647, $0.1<P<0.2$). The frequency distribution of residuals approximated a normal distribution, although not as well as those of the fall survey. An outlier from stratum 21u in 1972 influenced the model's estimates of abundances for that stratum; estimates were 60% greater than they would have been had this value been excluded from the analysis. A higher proportion of haddock on the Canadian side would have resulted if this value had been excluded. This stratum, however, does not contribute substantially to the overall abundance; therefore its impact was not studied further. The relative abundances between strata as characterized by the strata coefficients from the multiplicative model are shown in Figure 3. Two Canadian strata sections, 21c and 16c, which have a depth range from 56 to 110 m, had the highest coefficients. Three strata sections with a high number of zero values, 17u, 18c and 18u, were not used in the model.

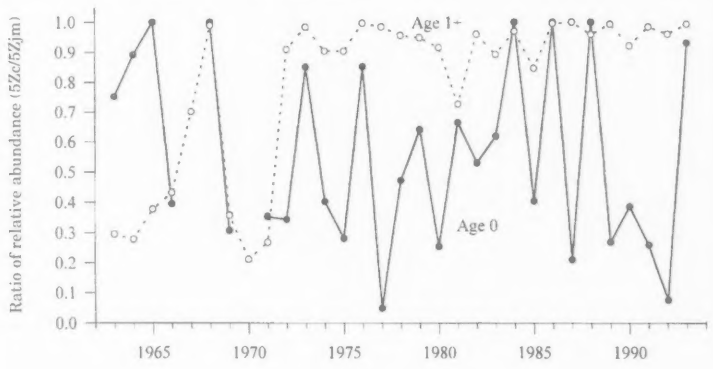


Figure 5

The distribution of haddock across the ICJ line in 5Zjm during the fall as indicated by the ratios of relative abundance from the NMFS fall survey.

The stratum and stratum section abundances from NMFS spring surveys are given in Table 2. Stratum section 16c, and 16u (secondarily), were again the highest contributors to total abundance. The relative contribution of stratum section 21c increased after 1976, whereas the contribution from stratum section 17c remained stable over time. As in fall, 19u in spring also declined in relative abundance from earlier times; very few haddock were caught there after 1981. The highest numbers in 19u were caught during 1980 and 1981. Haddock were virtually absent from 18c in spring but in the fall there were almost always some to be found there. Total abundance on the Canadian side was augmented by estimated numbers only four times, whereas most years were augmented for the U.S. side. The contribution made by these values to abundance on the U.S. side, however, was negligible.

Abundances by stratum for the DFO spring survey are given in Table 5. Haddock were always more abundant on the Canadian side than on the U.S. side; the Canadian side had 61–99% of the abundance in 5Zjm. Except for two occasions, haddock were more abundant in the shallower 5Z2 stratum than in the deeper 5Z1 stratum. Stratum 5Z2 and 5Z4 have the

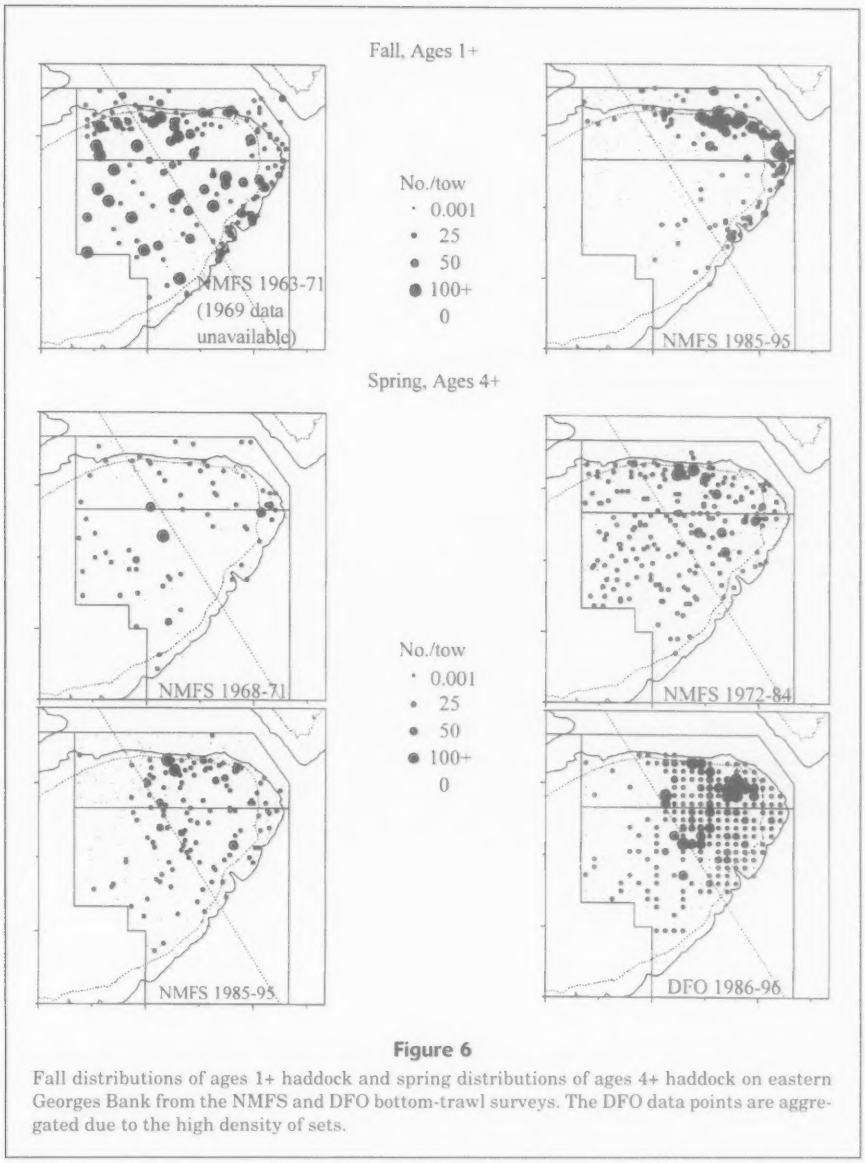


Figure 6

Fall distributions of ages 1+ haddock and spring distributions of ages 4+ haddock on eastern Georges Bank from the NMFS and DFO bottom-trawl surveys. The DFO data points are aggregated due to the high density of sets.

same depth range but, except for 1993, haddock were much more abundant in 5Z2.

The ratio of relative abundance trends from both the NMFS spring survey and the DFO spring survey indicated that haddock abundance is generally greater on the Canadian side of the ICJ line, though not as high as during the fall (Fig. 4). There was no obvious pattern by age in the ratios of abundance. The results of Friedman's test confirmed that there was not a significant age effect in the DFO spring survey but indicated that there were significant differences by age in the NMFS survey (Table 4). There was a tendency for lower ratios as age increases but the relationship was very weak (r^2=0.083 for ages 4–9+). Similarities in ratios of relative abundance among ages were examined with a correlation test of arcsine-transformed NMFS survey ratios. This revealed that age 1 did not correlate with any other ages (r<0.5), ages 2 and 3 showed some correlation with adjacent age classes, and ages 4–8 were highly correlated (r>0.5; Fig. 7). The ratios were plotted as three groups in Figure 8. For ages 4–8, there was

Table 5

Estimated abundance (numbers in thousands) of haddock by stratum on the Canadian and U.S. sides of the ICJ line in unit areas 5Zj and 5Zm (eastern Georges Bank) from spring Canadian Department of Fisheries and Oceans bottom trawl surveys.

	Canadian side		U.S. side		Total abundance	
Year	5Z1	5Z2	5Z3	5Z4	Canadian side	U.S. side
1987	3794	7162	103	40	10,956	143
1988	1398	12,444	5344	483	13,842	5827
1989	1874	9117	279	120	10,991	399
1990	4038	9903	1814	4214	13,941	6028
1991	2243	7961	3674	2429	10,204	6103
1992	4694	5540	2508	1507	10,234	4015
1993	2946	1879	37	2988	4825	3025
1994	15,424	11,091	167	180	26,515	347

more variability in the ratios from year to year than in the fall survey, but high values predominated except from the 1968–71 period when the ratios were lower. Ratios for age 1 were variable with no obvious tendency but most ages 2 and 3 ratios were greater than 0.5. The short length of the DFO survey series precluded investigation of this feature for these data.

The effect of total 5Zj,m abundance on the spring ratios of relative abundance was examined for this period because the greatest amount of dispersion onto the bank occurs during spring. This was evaluated by plotting the NMFS spring survey ratios of relative abundance against the beginning of year population numbers aggregated into three age groupings: age 1, ages 2 and 3, and ages 4–8. Population numbers were obtained from the 1995 eastern Georges Bank haddock assessment (Gavaris and Van Eeckhaute, 1995). No relation between abundance and ratios of relative abundance was apparent. The DFO time series was not investigated for this effect because of its short time span.

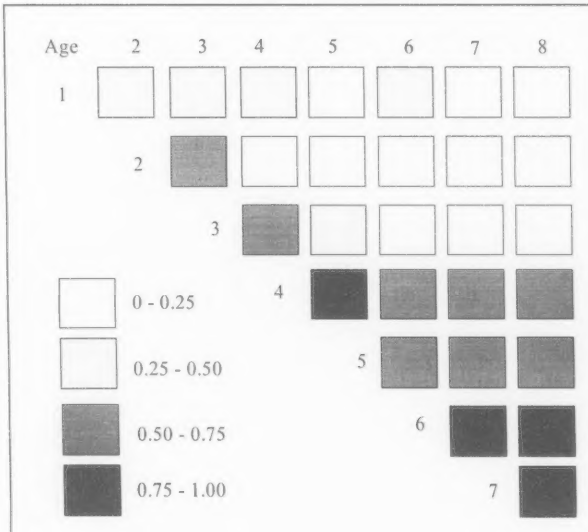


Figure 7

Age by age correlation of haddock ratios of relative abundance from the NMFS spring survey.

The distribution of age 4+ haddock determined by using the catch-per-tow data from the DFO spring survey pooled over 1986 to 1996 and the NMFS spring survey pooled over 1968–71, 1972–84, and 1985–95 are shown in Figure 6. During the 1972–84 and 1985-95 period (1986–96 for the DFO survey) there were aggregations throughout the Canadian side of 5Zj,m, especially in the area of the northeast peak, whereas the U.S. side showed lower abundance. This was especially evident for the 1985–95 period, but there were a number of occurrences of haddock along the southern flank of the bank in this period also. The spring distribution from 1968 to 1971 was markedly different from the recent distribution pattern. The northeast peak aggregations were not seen, and haddock seemed to be distributed uniformly throughout 5Zj,m. The distribution pattern during this period was strongly influenced by the exceptionally abundant 1963 year class.

Instantaneous rates of net migration

Haddock landings by the U.S. and Canadian fisheries have been affected by the spawning closure area

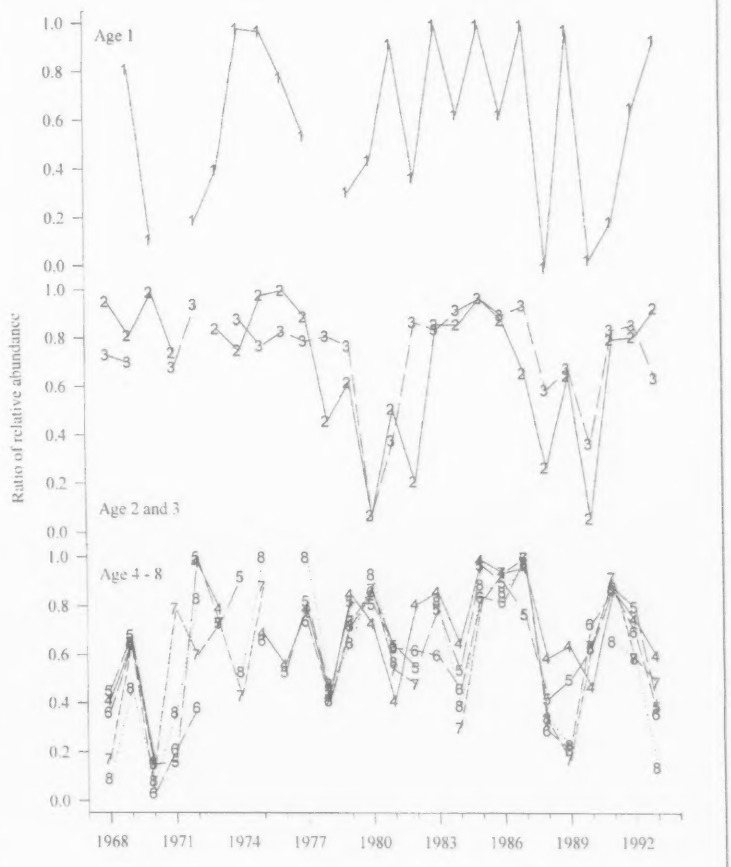


Figure 8

Relative abundance of haddock on the Canadian side of 5Zj,m by age group from the NMFS spring survey. Ratios were determined as abundance on Canadian side to total abundance in 5Zjm.

which was first instituted in 1970 by the International Commission for the Northwest Atlantic Fisheries and which was retained by both countries following extension of jurisdiction in 1977 (Halliday, 1988). The closure, which was put into effect from March to April during 1970–71, was extended to include May in 1972 and at that time an exemption for hook fisheries was introduced. In 1987 the United States extended the period to include February and in 1993, it was further extended to include January through June. The Canadian bottom trawl fishery has traditionally had limited activity during January and February except during 1991–93. Since 1985, when Canada and the United States have conducted haddock fisheries only on their respective sides of the ICJ line, the U.S. monthly catch of haddock in unit areas 5Zj,m (Fig. 9) generally have increased from January to June, but a sharp decline in landings occurred in July and the months following. Canadian landings peaked in June and July, the first two months following the spawning closure period, and decreased gradually to November.

The 6-month net migration rates calculated for three age groups (age 1, ages 2 and 3 combined, and ages 4 to 8 combined) displayed a persistent seasonal pattern indicating net movement towards the U.S. side between October and April followed by a return to the Canadian side between April and October (Fig. 10). Age-1 haddock had the greatest net migration rate to the Canadian side from April to September but also the

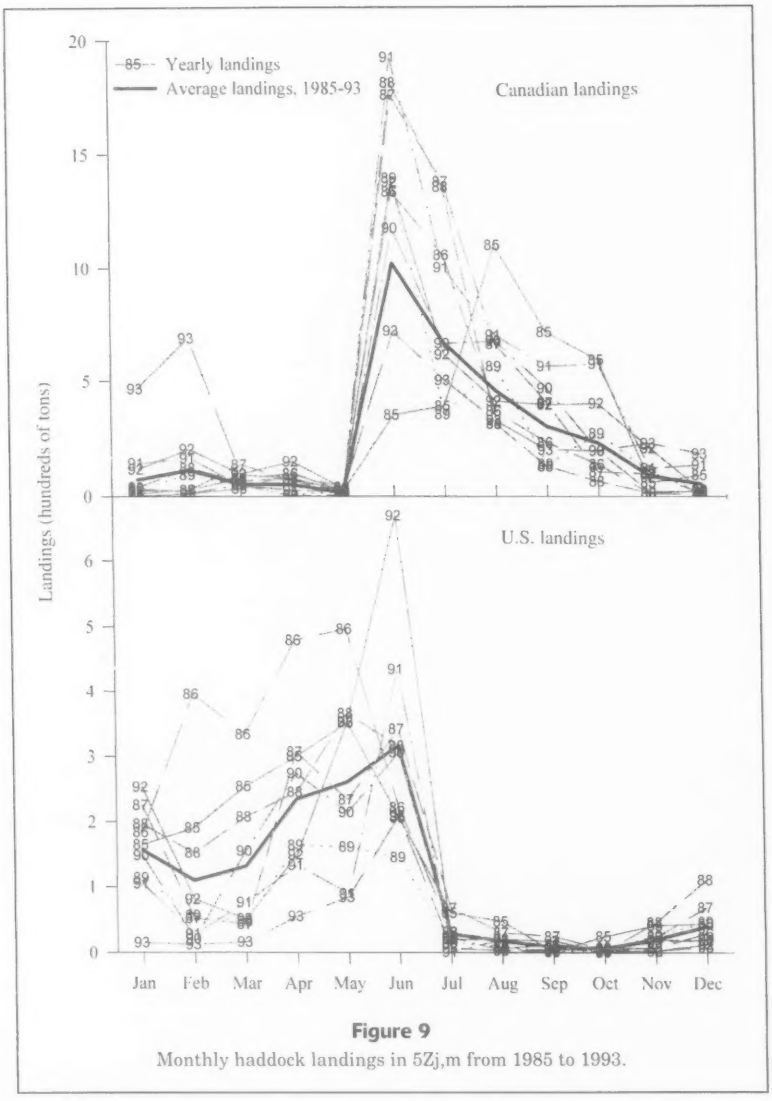


Figure 9
Monthly haddock landings in 5Zj,m from 1985 to 1993.

most variable.The net migration rate towards the U.S. side from October to March was often lowest at age 1, intermediate at ages 2 and 3, and greatest at ages 4 and older. By ages 4+ net migration back and forth seemed to be balanced. This general pattern was supported by the migration rates for the entire period examined, but the trend was less distinct from April 1985 to October 1987 than from April 1988 to October 1993. Examination of the spring ratios of relative abundance showed very high values during 1985–87 for ages 4–8 haddock (Fig. 8), indicating that there was not much movement across the ICJ line during that period.

Figure 11, which shows the movement and removals of a weak and a strong year class, the 1984 and 1985, respectively, for ages 1 and older, illustrates the migratory nature of the 5Zj,m stock across the ICJ line. The migratory pattern is well illustrated; a portion of the stock moved to the U.S. side from October to March and most of the stock moved back to the Canadian side from April to September. In spring the abundance on the Canadian side remained higher than on the U.S. side. The U.S. catch often consisted primarily of fish that had moved across the ICJ line from the Canadian side to the U.S. side and is indicated in the figure by the arrows pointing to the left.

No obvious pattern between net migration rates and population abundance was found. The range of abundance, however, for this period was very limited.

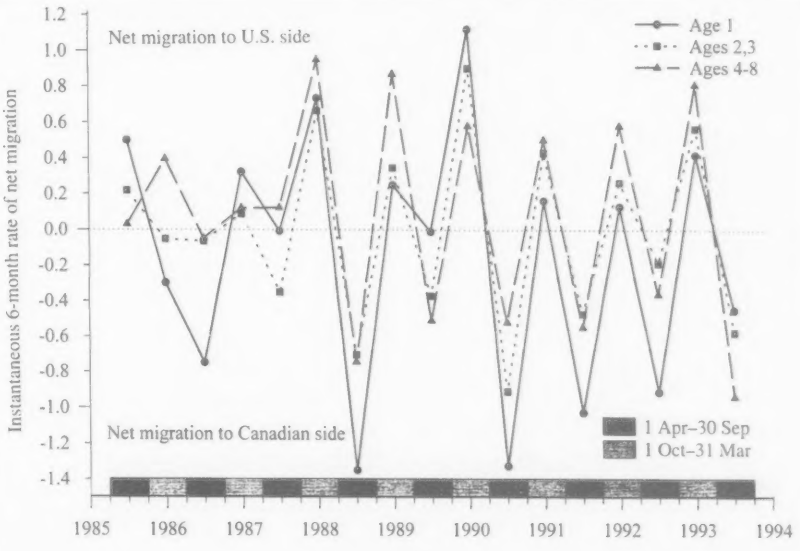


Figure 10

Net migration rates (expressed as annual rates) across the ICJ line for 6-month time periods for 5Zj,m haddock. These rates show that from April to September, net haddock migration was towards the east resulting in almost all haddock in 5Zj,m residing on the Canadian side in the fall. There was then a migration westward and across the ICJ line from October to March, a migration associated with spawning activities.

Discussion

Observations regarding haddock spatial distribution on Georges Bank during an earlier period (Colton, 1955) and for two dominant year classes more recently (Overholtz, 1985) have indicated that adult haddock are more abundant off the bank in deeper waters during the fall but are found on the bank in shallower waters during the spring. Colton (1955) reported that during spring, the greatest concentrations of larger haddock occur in water less than 110 m and presumed this was related to spawning activities. Migration from shallower water in spring to deeper water in the fall appears to occur by the end of July. Colton (1955) reported that few haddock of any age were found between 110 m and 165 m during the July–August surveys undertaken in 1949 and 1950. Older haddock, age 5+, could be found in waters deeper than 165 m in unit areas 5Zg,h and j. Overholtz (1985) also suggested that survey distributions of age-2 haddock indicated a movement by summer to deeper water in relation to the shallower depths generally occupied in spring. Colton (1955) and Overholtz (1985) reported some segregation of ages as fish moved into deeper water, i.e. older fish occupied deeper water than did younger fish, but Colton (1955) observed that in spring there appeared to be less segregation of age groups.

Although we observed two distinct distribution patterns over time within 5Zj,m, our analysis indicates that the depth-related patterns described above were persistent. The 1963–71 distribution pattern will be discussed more fully later in this section. Patterns observed from 1972 to recent times show that adult haddock in 5Zj,m were broadly dispersed over the bank during the spring period, their distribution extending westward of the ICJ line especially along the southern flank of Georges Bank. The NMFS strata with the highest densities in the spring were the Canadian portions of 21 and 16 which have a depth range from 56 to 110 m. The ratios of relative abundance, especially those from the DFO survey, clearly show that the majority of age-2+ haddock occupied waters within the Canadian jurisdiction at that time. Both NMFS and DFO spring surveys exhibit similar distribution patterns with similar areas of concentration. During the fall, haddock distribution shifted to the east onto the deeper bank slopes and few haddock remained on the U.S. side of the ICJ line. The ratios of relative abundance indicate that virtually all age 1+ haddock within 5Zj,m are on the Canadian side of the ICJ line in the fall.

The net migration results suggest that the westward migration of age-2 and older haddock in the winter–spring period is matched by a corresponding eastward migration during the summer–fall period of roughly similar magnitude. The net result is that roughly 20% to 25% of the adult haddock move across the ICJ line during a cycle. There may be a tendency for older haddock to migrate back and forth across the boundary line in greater numbers than for younger haddock because the instantaneous rates of net migration during the winter period for ages 4–8 are often greater than for younger ages, i.e. six out of nine times (Fig. 10). No relationship was found between stock abundance and the 1985–93 spring net migration rates, or the 1968–93 spring ratios of relative abundance, when a greater range in stock abundance occurred. The variability seen in the magnitude of movement to the U.S. side in spring from year to year (Figs. 8 and 10) may reflect variation in the timing of migration, variation in the magnitude of migration, sampling variation, or immigration from another source. Improved understanding of the source of this variability and better estimates of the magnitude and extent of migration may be possible from repeated surveying during the winter–spring period.

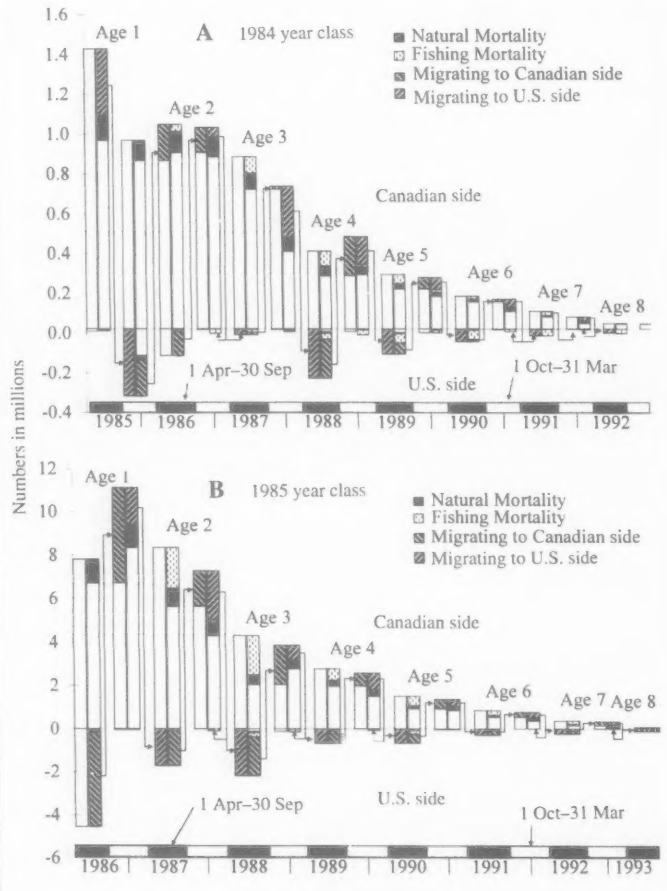


Figure 11

History of the (**A**) 1984 and (**B**) 1985 haddock year classes in unit areas 5Zj,m. The first bar of each pair represents the population size at the beginning of each 6-month period with the numbers gained from migration, if any. The second bar indicates the numbers lost to natural mortality, fishing mortality and migration to the other side of the ICJ line. The number of haddock left over at the end of the time period is represented by the unshaded portion of the second bar. The haddock that migrated across the ICJ line are added to the population or contribute to fishing mortality on the side they are migrating to during the same time period.

Distribution and migration show differences by age. The distribution of age-0 haddock was found to be different from that of older haddock, as has been previously described (Overholtz, 1985; Lough and Boltz, 1989; Polacheck et al., 1992). Haddock eggs and larvae spawned on the northeast peak may be distributed as far south as the Middle Atlantic Bight (Polacheck et. al., 1992). The ratios of relative abundance of age-0 haddock during fall are very variable and abundance often favors the U.S. side. There was a pattern of strong year classes being more abundant on the U.S. side whereas the weak year classes that followed were more abundant on the Canadian side. Additional research is needed to determine whether there is a mechanistic explanation for this observation. Our results suggest that the distribution and movement of age-1, -2 and -3 haddock differ from those of older haddock. In spring there was some correlation of ratios of relative abundance such that age-4 and older haddock had similar patterns and age-2 and age-3 haddock were similar whereas age-1 haddock did not correlate with any other ages. The differences likely reflect different migration patterns of immature and mature haddock. Maturity rates increase from ages 1 to 3 and by age 4 all haddock are mature (O'Brien and Brown, 1996; Trippel et al., 1997).

Haddock biomass (age 2 and older) on all of Georges Bank from 1935 to 1960 averaged 153,000 meteric tons (t). In

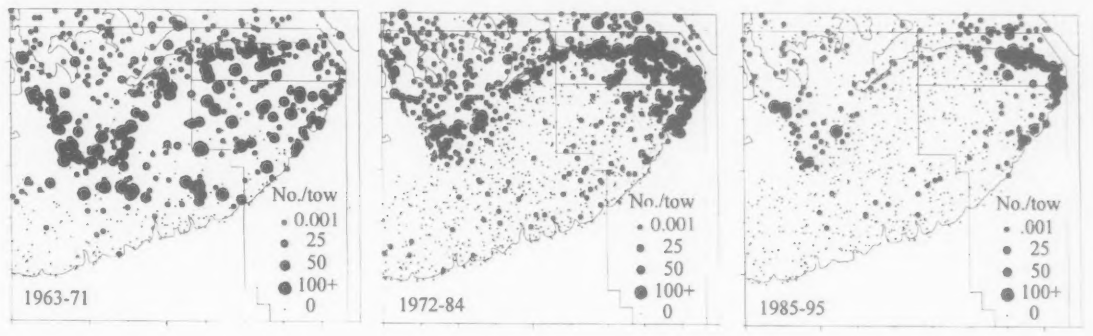


Figure 12

Fall distribution of age 1+ haddock on Georges Bank from NMFS bottom-trawl surveys. Data have been aggregated for the three time periods shown. Note that 1969 data are not included as these data were unavailable.

1965, biomass peaked at 427,000 t due to the recruitment of the "very strong" 1962 and the "outstanding" 1963 year classes that continued to dominate the population during the late 1960s and early 1970s (Clark et al., 1982). There was a large decline, by an order of magnitude, in the biomass of haddock on Georges Bank during the late 1960s and the early 1970s to a low of 14,000 t in 1973 (Clark et al., 1982). The fall distribution pattern during this period of exceptionally high but rapidly decreasing abundance indicates that haddock within 5Zj,m were more widely dispersed over the bank from 1963 to 1971 (Fig. 6) than that which was observed subsequently. Moreover, the ratios of relative abundance did not strongly favor the Canadian side of the ICJ line during 1963–71 (Figs. 4 and 5). This difference in distribution was also evident in the spring distribution pattern for ages 4 to 8 (Fig. 6) and in the spring ratios of relative abundance that were generally less than 0.5 during 1968–71 (Fig. 8). After this period, the ratios, though variable, were usually above 0.5. Polacheck[2] noted that haddock, since the late 1960s, were almost never caught in research survey tows in the southern and central portions of Georges Bank, areas where they had been caught regularly during the mid-1960s.

The post-1971 ratio of relative abundance trends for haddock persist to the present. During the late 1970s and early 1980s, the 1975 and 1978 year classes dominated the population and since then there have been several moderately strong year classes, i.e. the 1983, 1985, 1987, and 1992 (O'Brien and Brown, 1996; Gavaris and Van Eeckhaute, 1997). Despite accompanying fluctuations in haddock abundance, the relative abundance pattern has not reverted to that observed from 1963 to 1971. Polacheck,[2] using percent zero tows and patchiness to explore spatial distribution of Georges Bank haddock, also observed that when abundance increased with the 1975 and 1978 year classes, the patterns in spatial distribution did not resemble those observed from 1963 to the late 1960s. The distribution pattern during that time period was influenced strongly by the exceptionally large 1963 year class and may not be typical of the stock when it was in a more stable state as during the 1935–60 period. Recognizing the two spawning components and the likelihood that haddock may display different spatial affinities depending on their origin, we hypothesize that the 1963–71 distribution patterns may have been the result of an unusually greater contribution of recruitment from the southwestern spawning component. On the other hand, since 1985, the southwestern spawning component has probably been depleted to a greater extent and may not be contributing to Georges Bank production to the degree that it did from the mid-1970s to mid-1980s. The depletion of the southwestern spawning component is well illustrated by the fall distribution in 5Ze of ages 1+ haddock for three time periods, 1963–71, 1972–84, and 1985–95 (Fig. 12). Note that the almost continuous distribution of haddock seen along the northern edge of the bank during the first two time periods is not apparent during the later time period.

Since 1985, the relative abundance across the ICJ line and the net migration rates have likely not been strongly affected by variations in the abundance of the eastern Georges Bank spawning component. However, these attributes may get distorted by dis-

[2] Polacheck, T. 1995. CSIRO, Division of Fisheries, P.O. Box 1538, Hobart, Tasmania 7001, Australia. Personal commun.

tributional overlap of the two spawning components if the abundance of the southwestern component increases. This overlap effect may be responsible for the higher abundance at ages 2 and 3 of the strong 1978 year class on the U.S. side in spring (Fig. 8). Note, however, that at ages 4 and older, abundance shifts to being higher on the Canadian side of 5Zj,m.

From the temporal and spatial patterns of distribution, ratios of relative abundance with respect to the ICJ line, net migration rates, and monthly landings statistics, we can infer then that a seasonal migration, probably associated with spawning behavior, occurs in 5Zj,m. This migratory behavior may be influenced by temperature conditions but, although temperature data is collected during surveys, the time range of this information is too limited to investigate the effect on migration timing. The westward movement of haddock onto the bank into shallower water probably begins around November and reaches its greatest extent to the west during the peak of spawning in March–April, after which the return migration eastwards begins. Most haddock have probably migrated eastward across the ICJ line by July and by October; haddock are found far east of the line preferring the deeper waters of the northeast slopes of the bank.

An understanding and appreciation of the distribution and migration patterns on eastern Georges Bank in relation to the ICJ line are important prerequisites for investigation of sustainable harvest practices for this transboundary resource. The pattern of migration described in our study does not alter sustainable levels for the area as a whole but because of the seasonal nature of exploitation by Canada and the United States, this information can provide guidance on the exploitable biomass available on each side during different seasons so that consistent and equitable harvest rates can be determined. After establishment of the international boundary, Canada and the United States have managed the resources in their respective territories with little attention to what was being done in adjacent waters. Though it has been suggested that sustainable fisheries could be maintained through independent management (Gavaris et al., 1993), it is likely that the greatest potential would be achieved through consistent management. Knowledge of temporal and spatial distribution patterns can form the basis upon which consistent management practices are explored.

Acknowledgments

We are grateful to the staff of the National Marine Fisheries Service at the Northeast Fisheries Center, Woods Hole, Massachusetts, for their provision of research survey and commercial landings data that permitted the preparation of this manuscript. We also thank especially Ralph Halliday and Russell Brown for their valuable comments on an earlier version of the manuscript and the two anonymous referees.

Literature cited

Beverton, R. J. H. and S. J. Holt.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food UK (series 2) 19, 533 p.

Bigelow, H. B., and W. C. Schroeder.
1953. Fishes of the gulf of Maine. U.S. Fish Wildl. Serv. Bull. 74, vol. 53, 577 p.

Clark, S. H., W. J. Overholtz, and R. C. Hennemuth.
1982. Review and assessment of the Georges Bank and Gulf of Maine haddock fishery. J. Northw. Atl. Fish. Sci. 3: 1–27.

Colton, J. B.
1955. Spring and summer distribution of haddock on Georges Bank. Special Scientific Report of the U.S. Fish and Wildlife Service—Fisheries 156, 65 p.

Cook, R. D.
1977. Detection of influential observation in linear regression. J. Statistical Society 74:169–174.

Gavaris, S.
1980. Use of a multiplicative model to estimate catch rate and effort from commercial data. Can. J. Fish. Aquat. Sci. 37:2272–2275.

Gavaris, S., and L. Van Eeckhaute.
1990. Assessment of haddock on eastern Georges Bank. Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) Res. Doc. 90/86, 37 p.
1991. Assessment of haddock on eastern Georges Bank. CAFSAC Res. Doc. 91/86, 30 p.
1994. Assessment of haddock on eastern Georges Bank. Canadian Dep. Fisheries and Oceans (DFO) Res. Doc. 94/31, 38 p.
1995. Assessment of haddock on eastern Georges Bank. DFO Res. Doc. 95/6, 36 p.
1997. Assessment of haddock on eastern Georges Bank. DFO Res. Doc. 97/54, 72 p.

Gavaris S., and L. Van Eeckhaute, M. I. Buzeta, and J. Hunt.
1993. Yield projections for the transboundary cod and haddock resources on eastern Georges Bank. Canadian Dep. Fisheries and Oceans (DFO) Res. Doc. 93/71, 19 p.

Grosslein, M. D.
1962. Haddock stocks in the ICNAF Convention Area. International Commission for the Northwest Atlantic Fisheries (ICNAF) Redbook Part III: 124–131.

Halliday, R. G.
1988. Use of seasonal spawning area closures in the management of haddock fisheries in the Northwest Atlantic. Northwest Atlantic Fisheries Organization (NAFO) Sci. Coun. Studies 12:27–36.

Halliday, R. G., and A. T. Pinhorn.
1990. The delimitation of fishing areas in the northwest Atlantic. J. Northwest Atl. Fish. Sci. 10:1–51.

Lough, R. G., and G. R. Bolz.
1989. The movement of cod and haddock larvae onto the shoals of Georges Bank. J. Fish Biol. 35(suppl. A):71–79.

O'Brien, L., and R. W. Brown.
1996. Assessment of the Georges Bank haddock stock for 1994. New England Fisheries Steering Committee (NEFSC) Ref. Doc. 95–13.

Overholtz, W. J.
1985. Seasonal and age-specific distribution of the 1975 and 1978 year-classes of haddock on Georges Bank. Northwest Atlantic Fisheries Organization (NAFO) Sci. Coun. Studies 8:77–82.
1987. Factors relating to the reproductive biology of Georges Bank haddock (*Melanogrammus aeglefinus*) in 1977–83. J. Northwest Atl. Fish. Sci. 7:145–154.

Polacheck, T., D. Mountain, D. McMillan, W. Smith, and P. Berrien.
1992. Recruitment of the 1987 year class of Georges Bank haddock (*Melanogrammus aeglefinus*): the influence of unusual larval transport. Can. J. Fish. Aquat. Sci. 49: 484–496.

Schuck, H. A., and E. L. Arnold.
1951. Comparison of haddock from Georges and Browns bank. Fish. Bull. 52:177–185.

Smith, S. J.
1988. Abundance indices from research survey data. *In* D. Rivard (ed.), Collected papers on stock assessment methods, p. 16–40. CAFSAC Res. Doc. 88/61.

Trippel, E. A., M. J. Morgan, A. Fréchet, C. Rollet, A. Sinclair, C. Annand, D. Beanlands, and L. Brown.
1997. Changes in age and length at sexual maturity of northwest Atlantic cod, haddock and pollock stocks, 1972–1995. Can. Tech. Rep. Fish. Aquat. Sci. 2157:xii +120 p.

Walford, L. A.
1938. Effects of currents on distribution and survival of the eggs and larvae of haddock (*Melanogrammus aeglefinus*) on Georges Bank. Bull. U. S. Bur. Fish. 49:1–73.

Abstract.—Growth of otoliths of adult widow rockfish, *Sebastes entomelas*, and yellowtail rockfish, *S. flavidus*, inhabiting the coastal waters off central and northern California was reduced in 1983. This reduction (12.6% and 20.5%, respectively) coincided with a strong El Niño event that dominated oceanographic conditions that year. Otolith growth from 1980 to 1987 was significantly correlated with ocean temperature, upwelling, and sea level anomaly. Specifically, in 1983, the highest ocean temperature, largest positive sea level anomaly, and lowest amount of coastal upwelling corresponded to the smallest mean otolith growth increment.

Reduction of growth in otoliths of widow and yellowtail rockfish (*Sebastes entomelas* and *S. flavidus*) during the 1983 El Niño

David Woodbury
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
3150 Paradise Drive
Tiburon, California 94920
E-mail address: David.Woodbury@noaa.gov

Manuscript accepted 16 September 1998.
Fish. Bull. 97:680–689 (1999).

In 1983, one of the strongest El Niño events of the century occurred in the east-central Pacific Ocean (Cane, 1983; Rasmusson, 1984; Glynn, 1988). This event had strong negative effects on the growth of many marine organisms inhabiting waters along the west coast of North America, including giant kelp (Zimmerman and Robertson, 1985), yellowtail rockfish (Lenarz and Wyllie Echeverria, 1986), coho and chinook salmon (Pearcy and Schoener, 1987), Pacific herring (Spratt, 1987), Pacific kelp (Germann, 1988), Pacific hake (MacLellan and Saunders, 1995), and blue rockfish (VenTresca et al., 1995).

Atypically narrow annuli (annual growth increments) formed during 1983 were observed during routine aging of otoliths from adult yellowtail rockfish, *Sebastes flavidus* (Fig. 1). Because otolith growth is generally proportional to fish growth, a reduction in the width of the 1983 annulus could correspond to poor fish growth caused by the El Niño-induced anomalous oceanographic and biotic conditions present that year. Widths of annually formed increments on the hard parts of animals and plants have been used to correlate growth with a range of environmental conditions. A common example is the relation between the widths of tree rings and annual precipitation. In the marine environment, a reduction in annual shell growth of geoduck clams was observed to correspond with increased pollution (Noakes and Cambell, 1992). Boehlert et al. (1989) used otolith annuli to provide historical time series of growth in *Sebastes* that were compared with environmental factors. In a similar study, MacLellan and Saunders (1995) noted a reduction in the 1983 annulus of Pacific hake otoliths inhabiting northeastern Pacific waters, attributing it to the negative effect of the 1983 El Niño.

In this study, otolith growth from 1980 to 1987 was measured from two commercially important rockfish species: yellowtail rockfish and widow rockfish (*S. entomelas*). These species range from British Columbia to southern California (Gunderson and Sample, 1980). They are semipelagic, associated with bottom structure located on the shelf. The measurements of otolith growth were compared with physical oceanographic variables collected during the same period.

Methods

Otolith growth

Otoliths from female yellowtail rockfish inhabiting Cordell Bank, California (Fig. 2), were collected during research cruises conducted from 1986 to 1992. As noted earlier, during otolith age determination procedures, the 1983 annulus was

observed to be narrower than adjacent annuli. To quantify this observation, measurements of annuli were made on these otoliths, as well as additional otoliths obtained from an ongoing port sampling program. Otoliths were collected from male and female widow and yellowtail rockfish landed at Eureka, California, and female widow rockfish landed at Bodega Bay, California, during 1989 and 1990.

The annulus was defined as otolith growth from the end of one summer to the end of the following summer (approximately October through September). Using reflected light on the distal surface of whole otoliths, I observed that summer growth appears as a white ring and winter growth as a dark ring (Fig. 1). Annuli from 366 otoliths were measured by using one of the two following methods. With the first method, a camera lucida was mounted atop a dissecting microscope, which was used to trace the surface annuli from 115 female yellowtail rockfish otoliths collected at Cordell Bank. A digitizing pad was used to measure the area of each annulus from the tracings. One or two otoliths per hour could be processed with this method. The remaining 251 otoliths were analyzed by using an image enhancement system comprising a personal computer interfaced with a dissecting microscope and a high resolution closed-circuit video camera. A mouse-driven crosshair was used to trace the annuli displayed on the monitor. This method increased production by sixfold. The area of each annulus (mm^2) was square-root–transformed prior to analysis. To compare the two methods, annuli from five otoliths measured by the first method were remeasured by using the second method. The differences in the estimated growth from these five otoliths ranged from 0.2 to 11.4%, with a mean of 2.9%, which represented a minor error compared with observed interannual growth differences.

Potential problems arise when measuring all the annuli in an otolith. When these rockfish species reach sexual maturity and somatic growth slows, the reduced growth rate is reflected in their otoliths. Therefore, it would be impossible to determine if a reduction in otolith growth was caused by poor environmental conditions or from energy being diverted into gonadal development. In addition, annuli formed after the onset of maturity are deposited disproportionately on the proximal surface of the otolith. It is easier to measure annuli deposited during the immature phase on the distal side of the otolith. To minimize these concerns, measurements were restricted to the five annuli formed prior to sexual maturity. Both male and female widow rockfish have an age of 50% maturity of five years, whereas male and female yellowtail rockfish are mature at six and seven years,

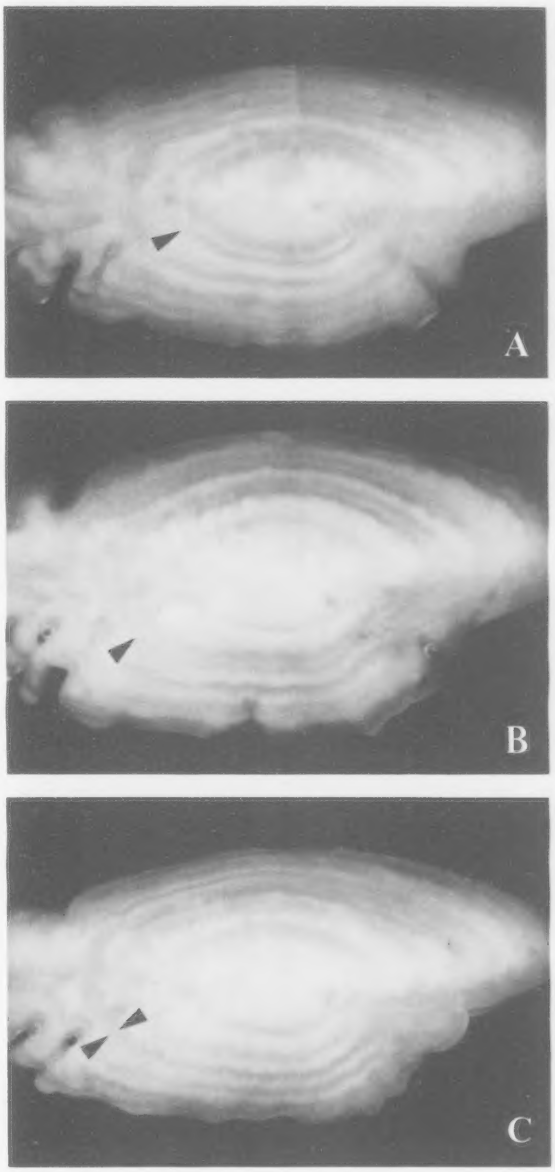


Figure 1

Otoliths from female yellowtail rockfish collected at Cordell Bank, California, showing narrow 1983 annulus (arrow): (**A**) 1982, (**B**) 1981, and (**C**) 1980 year classes.

Table 1

Sample sizes for each combination of rockfish species, port, sex, and yearclass.

			Yearclass					
Species	Port	Sex	1979	1980	1981	1982	1983	Total
Yellowtail	Eureka	Female	2	22	10	6	11	51
Yellowtail	Eureka	Male	1	27	19	1	10	58
Yellowtail	Cordell Bank	Female	16	38	47	13	1	115
Widow	Eureka	Female	9	9	22	11	1	52
Widow	Eureka	Male	12	10	21	11	4	58
Widow	Bodega Bay	Female	7	4	15	6	0	32
Total			47	110	134	48	27	366

respectively (Wyllie Echeverria, 1987). An additional concern arises from the protracted parturition season exhibited by these species. Interannual differences in birthdate distributions (Woodbury and Ralston, 1991) result in interannual differences in otolith growth during the first year of life. Therefore, measurements of the first annulus were not included in the analysis because they might have biased the data. Only measurements of otolith growth for the years 1980–87, comprising ages 1–4 and otoliths from fish belonging to the 1979–83 year classes (Table 1) were used.

The results of this study are dependent upon the accuracy of the ages assigned to each otolith. It is not uncommon for ages to vary by one or more years between readers or among readers re-aging the same otolith. The 1983 annulus was observed over a period of several years during which one additional annulus was deposited each subsequent year for year classes prior to 1983. By using the distinctive 1983 annulus (Fig. 1) as a natural tag (MacLellan and Saunders, 1995), I was able to assign an age to each otolith in this study that was accurate.

To test the validity of the 1983 annulus in this study, twelve otoliths that had previously been aged were re-examined without knowledge of their date of capture. On the basis of only the pattern of annuli widths, 11 of the 12 otoliths were assigned to their previously determined year class. The one misinterpretation was for an otolith from a fish born in 1984, which did not have the 1983 annulus. This error would be unlikely in the data used for this study because the otoliths were first aged by the break-and-burn method, in which the year of birth was determined from counting all the annuli. The narrow 1983 annulus could then be used to ensure that the correct age was obtained.

The following additive model (Weisburg, 1993) was used to calculate treatment effects on annual otolith growth for each species over all years.

Figure 2

Sampling locations at Eureka, Bodega Bay, and Cordell Bank.

$$\Delta_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_k + \delta_l + \varepsilon_{ijkl},$$

where Δ_{ijkl} = index of annual otolith growth of a species;
μ = mean square-root of annual growth;
α_i = year "i" fixed effect;
β_j = age "j" fixed effect;
γ_k = port "k" fixed effect;
δ_l = sex "l" fixed effect; and
ε_{ijkl} = normal error term.

This model assumes no significant interaction among any of the four main effects. This assumption was evaluated in Figures 3 and 4, where annual least-square means are plotted against year for each species-sex-port combination by using both a combined model with no interaction term for the age-by-year

effect, and a model with interactions that estimates a distinct otolith growth effect for each age-by-year combination. These figures show that although there are statistically significant interactions, the signal for the year effect is not strongly effected by excluding the interaction terms from the model. The additional variance explained by the model with interactions was only 3.5% and 4.2%, for yellowtail and widow rockfish, respectively. Because inclusion of an interaction term contributes little to the explanatory power of the model, and analyses that include interaction terms are much more restrictive in terms of data requirements, the simple, combined additive model was used, thereby allowing the computation of a longer time series of annual otolith growth effects (1980–87).

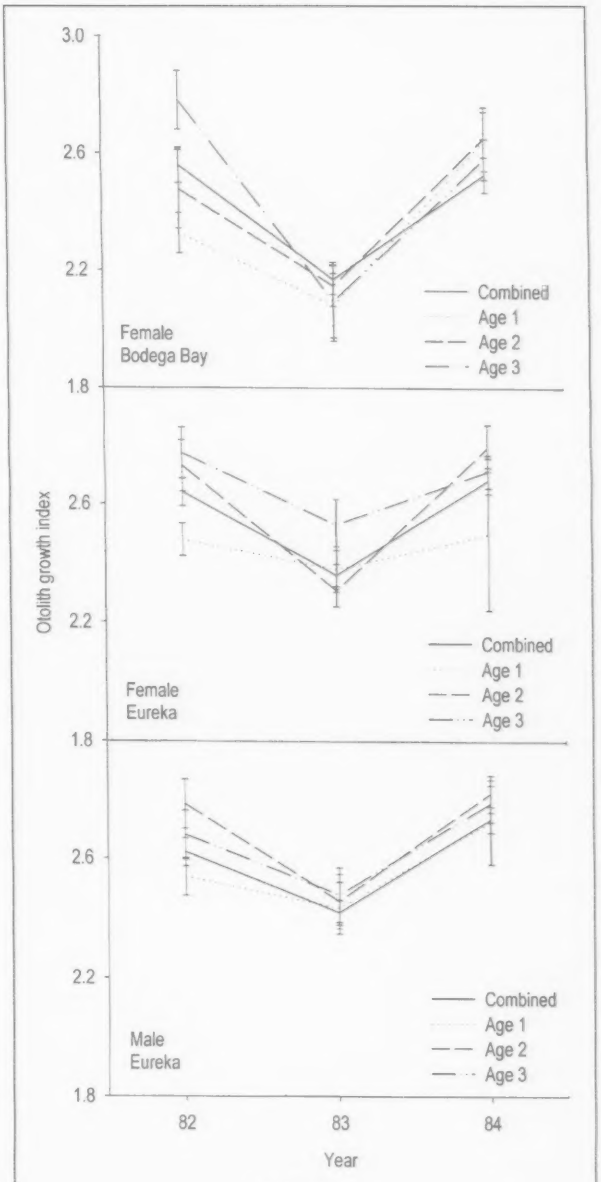


Figure 3

Comparison of mean annual otolith growth indices (1982–84) among models with and without interaction terms for widow rockfish. Bars represent ±1 standard error of the mean.

Oceanographic databases

Thirteen oceanographic variables were analyzed to determine their relation with otolith growth patterns. These included eight measures of ocean temperature, three upwelling indices, a sea level statistic, and the northeast Pacific atmospheric pressure index. All ocean temperature data were obtained from the Fleet Numerical Oceanography Center, Master Oceanographic Observations Data Set (Sharp and McClain, 1993). The data included temperature at the sea surface, at 100 m, at 200 m, and the depth of the 10°C isotherm. Measurements were summarized from two coastal areas (i.e. 36–39°N × 121–125°W and 39–42°N × 123–127°W), which together encompass the region where the fish were collected. Annual means for 1980–87 were calculated from the monthly means of October through September, the otolith growth year as defined in this study. Annual upwelling indices (Bakun, 1975) were calculated from daily upwelling statistics. In this instance, the mean of the February to April monthly means was computed, as these three months bracket the spring transition (Strub et al., 1987) when nutrient-rich water is first upwelled to the surface, initiating the biological production cycle (Cushing, 1975). Upwelling data were summarized from three localities (i.e. 36°N, 39°N, and 42°N), which represent the area of fish collections. Sea level data compiled at the San Francisco tidal station were used to compute monthly anomalies, after correcting for differences in atmospheric pressure (University of Hawaii[1]). Annual mean sea level anomalies were then calculated from the monthly means of October through September. Lastly, the northeast Pacific atmospheric pressure index is an indicator of atmospheric forcing upon ocean waters (Beamish and Bouillon, 1993). This index is the mean monthly difference in surface atmospheric pressure between 40°N, 120°W (Reno,

[1] Sea Level Center, Univ. Hawaii, Honolulu, Hawaii. 1994. Unpubl. data.

Nevada) and 50°N, 170°W (Aleutian Islands) (NOAA[2]). A plot of the data revealed an increase in the intensity of the pressure differences during the winter months. Therefore, annual means were calculated from the monthly means for November to March.

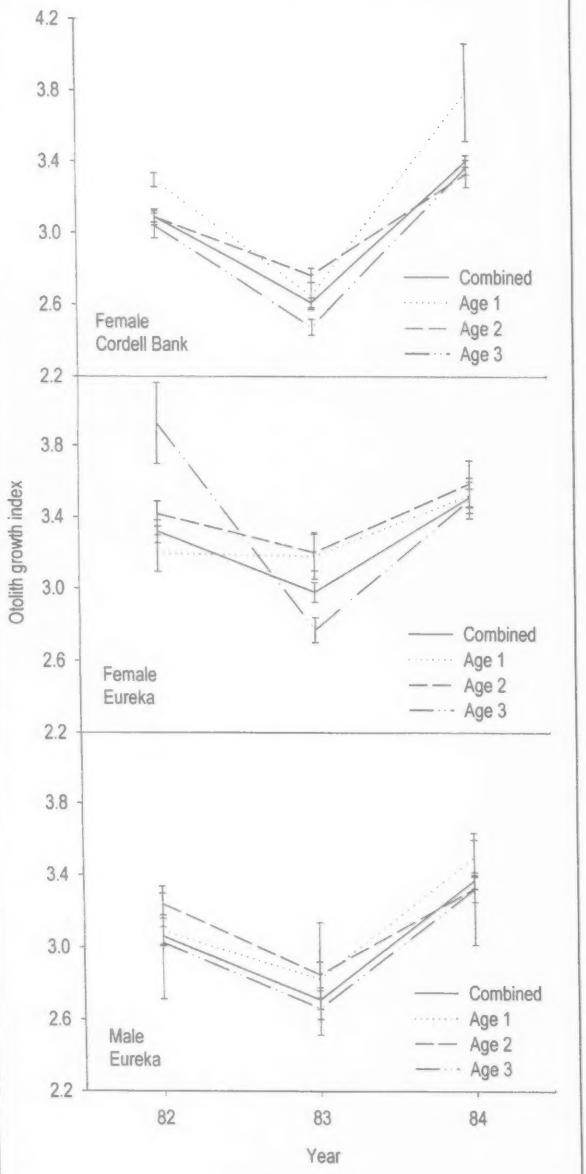


Figure 4

Comparison of mean annual otolith growth indices (1982–84) among models with and without interaction terms for yellowtail rockfish. Bars represent ±1 standard error of the mean.

Owing to strong interdependence among these 13 oceanographic variables, a principal component analysis (SAS Institute Inc., 1988) was conducted to reduce the dimensionality of the information and to insure statistical independence of the data. The ordination was conducted on the correlation matrix, so that each variable was weighted equally. The otolith data were then compared with the principal components of the oceanographic data to quantify the impact of the 1983 El Niño event on the growth of yellowtail and widow rockfish otoliths.

Results

Patterns of annual otolith growth were similar in widow and yellowtail rockfish from 1980 to 1987 (Fig. 5). A 12.6% and 20.5% reduction in otolith growth occurred during 1983 for widow and yellowtail rockfish, respectively. This year of reduced otolith growth was followed by enhanced growth, especially for yellowtail rockfish. The growth estimates calculated for 1980 and 1987 were based on samples from one year, i.e. the 1979 and 1983 year classes respectively, and these estimates should be viewed with caution.

Although most of the variance in otolith growth is explained by the year effect, the other effects in the model are worth noting (Table 2). There was a significant difference in otolith growth between sexes for yellowtail rockfish (i.e. otoliths from females grew faster than those from males); however, this was not the case for widow rockfish. Growth of the otolith at age differs between species (Fig. 6), which may be the result of somatic growth rate differences between the species. In a simple simulation, similar curves were produced by varying the von Bertalanffy growth coefficient (k). Yellowtail rockfish exhibit faster growth than do widow rockfish, thus yielding relatively lower indices of otolith growth with increasing age. There was a significant difference in otolith growth between the two ports for both species (i.e. otoliths from fish collected in Eureka grew faster than those from Bodega). Further analysis revealed that these differences began in 1983. Figure 7 shows results of four separate ANOVAs run on each of the four species-port combinations. In these analyses, sex and port were excluded as effects in the model. Otolith growth was similar at the two ports prior to 1983. Al-

[2] Pacific Marine Environmental Laboratory, National Oceanic and Atmospheric Administration, Seattle, Washington. 1994. Unpubl. data.

Table 2

Analysis of variance results for the growth model used in this study.

Source	df	Sum of squares	Mean square	*F*-Value	*P*>*F*
Widow rockfish (r^2=0.318)					
Model	12	19.9617	1.6635	21.57	0.0001
Year	7	13.6558	1.9508	25.29	0.0001
Age	3	2.3318	0.7773	10.08	0.0001
Port	1	0.9860	0.9860	12.78	0.0004
Sex	1	0.1064	0.1064	1.38	0.2408
Error	555	42.8046	0.0771		
Corrected total	567	62.7663			
Yellowtail rockfish (r^2=0.542)					
Model	12	96.8742	8.0728	87.09	0.0001
Year	7	77.8370	11.1196	119.96	0.0001
Age	3	3.3136	1.1045	11.92	0.0001
Port	1	3.5704	3.5704	38.52	0.0001
Sex	1	3.8560	3.8560	41.60	0.0001
Error	883	81.8491	0.0927		
Corrected total	895	178.7233			

though both species exhibited significant reduction in otolith growth in 1983, the effect was more pronounced at Bodega, consistent with a decreasing effect of El Niño with increasing latitude, as was observed in Pacific hake (MacLellan and Saunders, 1995). Although otolith growth recovered quickly for both species at Eureka and for yellowtail rockfish at Bodega, otolith growth for widow rockfish collected from Bodega was relatively slow to recover.

Results of the principal component analysis on the oceanographic data (Table 3) show that only the first two components are very informative (eigenvalue ≥1; first three principal components shown). Note that the first component explained 70% of the combined variation among all 13 oceanographic variables, whereas the second component accounted for an additional 18%. As the loadings on the first principal component indicate, temperature and sea level anomaly are closely linked. Upwelling loads higher with increasing latitude, which may relate to increased upwelling from south to north along that section of coast. Upwelling also demonstrates an inverse relation with temperature and sea level anomaly. Finally, the atmospheric pressure statistic does not contribute substantially to the first principal component, although it is much more influential in the second component.

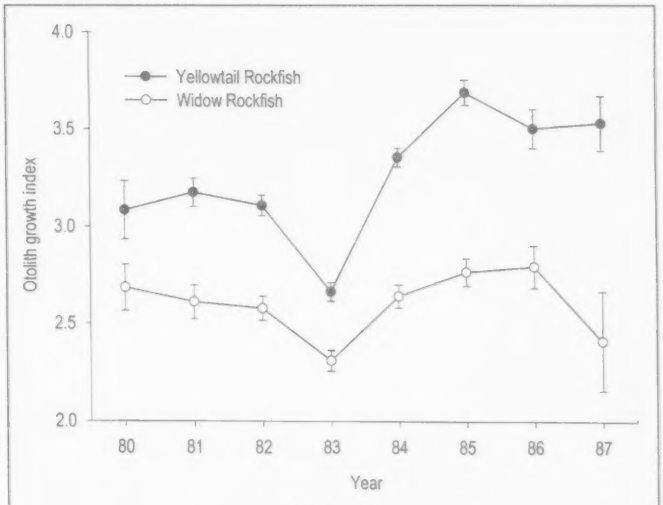


Figure 5

Mean annual otolith growth indices (1980–87) for each species. Bars represent ±2 standard errors of the mean.

A multiple regression of otolith growth on the first two principal components showed that the second component was neither significant nor informative, and it was therefore dropped from the analysis. An ordinary regression of otolith growth on the first principal component resulted in a significant relationship for both widow and yellowtail rockfish (P=0.033

and 0.030, respectively). Plots of mean annual otolith growth index against the first principal component score (Fig. 8) reveal the extreme conditions that prevailed in 1983. In 1983, the lowest measurements of otolith growth corresponded to the highest sea temperature, highest positive sea level anomaly, and lowest upwelling index. As previously noted, this particular El Niño was one of the strongest on record for the east-central Pacific Ocean. Its signature was noted off the California coast by high sea temperature at 100 m, being the warmest observed since records were first kept starting in 1944 (Sharp and McClain, 1993). A converse relationship between enhanced otolith growth and lower sea temperature, lower sea level anomaly, and higher upwelling index is not as evident, although above normal growth did occur in 1985, which was the "coldest" year.

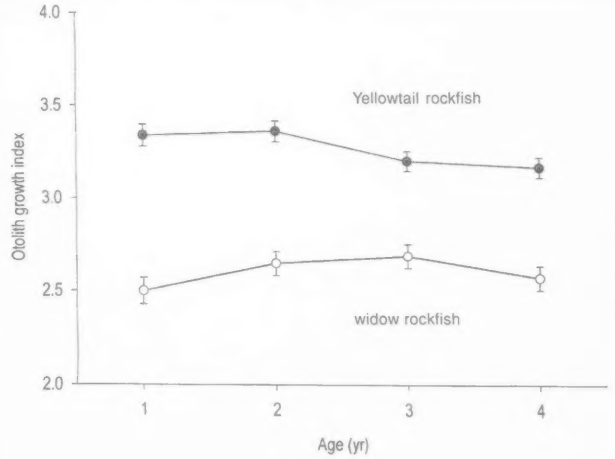


Figure 6

Mean otolith growth indices at age for widow and yellowtail rockfish. Bars represent ±2 standard errors of the mean.

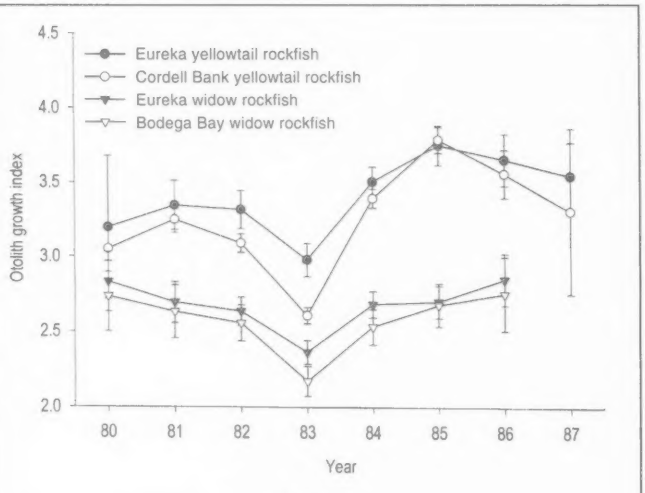


Figure 7

Mean annual otolith growth indices (1980–87) for widow and yellowtail rockfish from two geographic areas. Bars represent ±2 standard errors of the mean.

Discussion

In this paper, the reduction in growth of widow and yellowtail rockfish otoliths during 1983 was quantified by measuring annuli surface areas. Otolith growth is postulated to represent a conservative measure of somatic growth. Casselman (1990) determined that otoliths from several species of freshwater fish grew relatively faster than their body during periods of slow body growth. Francis et al. (1993) argue that otolith growth in *Pagrus auratus* can occur even if somatic growth has stopped. Therefore, the reduction observed from this study may indicate an even larger reduction in somatic growth, perhaps affecting reproductive capacity as well. This was observed by VenTresca et al. (1995) who noted a reduction in both the somatic and gonadal indices of blue rockfish (*S. mystinus*) inhabiting California coastal waters in 1983.

It appears that the oceanographic perturbations caused by El Niño had a negative effect on the growth of these fish. Temperature has been implicated as a major contributor to influencing both otolith and somatic growth. Lombarte and Lleonart (1993) stated that environmental conditions, mainly temperature, regulate the quantity of material deposited during the formation of the otoliths. Dorn (1992) found that growth of Pacific whiting (*Merluccius productus*), which inhabit similar waters, is most affected by temperature during younger ages.

Although physical oceanographic conditions and otolith growth were found to be significantly correlated, the causal relationship may well be based on preferred food availability. Central California represents the southernmost range of both widow and yellowtail rockfish. Pearson and Hightower (1991) reported slower

growth of widow rockfish in this area as compared with growth from more northerly distributed populations. This may be related to diet because more northerly distributed populations consume more fish and euphausiids, whereas populations in the south feed more on gelatinous zooplankters. Lorz et al. (1983) reported the diet of yellowtail rockfish in Queen Charlotte Sound comprised both fish and euphausiids, whereas off Washington it comprised mainly euphausiids. Pereyra et al. (1969) found that fish dominated the diet of both yellowtail and widow rockfish collected near Astoria Canyon, off northern Oregon. Brodeur and Pearcy (1984) noted that yellowtail rockfish preyed on a diverse assemblage, dominated by euphausiid, fish and squid, depending on the season. Adams (1987) reported that widow rockfish collected off northern California fed primarily on gelatinous zooplankters. At Cordell Bank, during late fall, winter, and in years of reduced productivity (e.g. 1983), yellowtail rockfish have been found to feed primarily on gelatinous zooplankton, which has a lower nutritional value than their preferred diet of euphausiids (MacFarlane[3]). Owing to the lack of upwelling and reduced productivity during 1983, these fish were probably forced to feed on less nutritional prey. Although lacking stomach analysis data for 1983, Lenarz and Wyllie Echeverria (1986) found a significant reduction in visceral fat of yellowtail rockfish collected at Bodega Bay during 1983 as compared with 1980, a "normal" year.

An assumption of this study is that the widow and yellowtail rockfish sampled during this study did not migrate to less productive waters during 1983 and then return. Most species within the *Sebastes* genus spend their adult life within a relatively small area (Stanley et al., 1994). Both widow and yellowtail rockfish lead an epibenthic schooling existence, inhabiting the area above benthic structures. Several tagging studies have been conducted on yellowtail rockfish to study the movement of these fish. Carlson and Haight (1972) noted homing behavior in yellowtail rockfish that were captured and transplanted to different areas in Alaska. Pearcy (1992) tagged 25 yellowtail rockfish on Heceta Bank off central Oregon and noted little displacement during a one-month period. However, Stanley et al. (1994) noted displacement of several tagged yellowtail rockfish from Alaskan and Canadian waters after they had been at large for several years. Although no tagging studies have been conducted on widow rockfish, it is worth noting

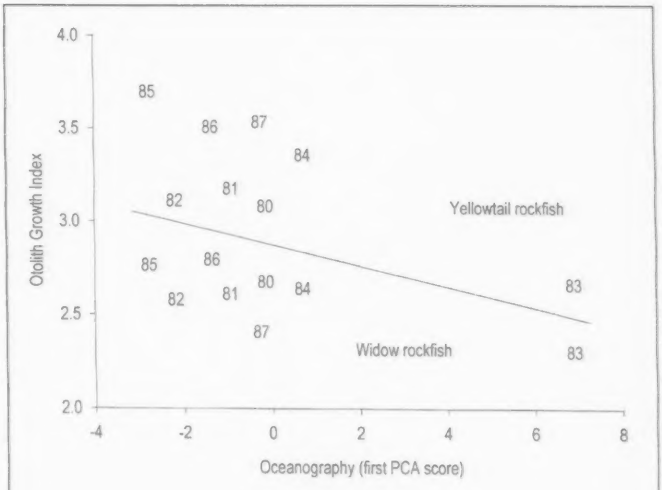


Figure 8

Mean annual otolith growth indices compared to the first principal component annual scores of oceanographic variables.

Table 3

Principal component analysis results for the thirteen oceanographic variables (1980–87).

	Principal component		
	1	2	3
Eigenvalue	9.10	2.36	0.96
Percent variance	70.0	18.1	7.4
Cumulative variance	70.0	88.1	95.5
Eigenvectors			
Sea surface temp at 39–42°N	0.259	0.269	–0.417
Sea surface temp at 36–39°N	0.287	0.255	–0.265
100 m temp at 39–42°N	0.313	0.119	0.276
100 m temp at 36–39°N	0.304	0.053	0.382
200 m temp at 39–42°N	0.302	–0.135	–0.321
200 m temp at 36–39°N	0.301	–0.165	–0.299
Depth of 10°C isotherm at 39–42°N	0.301	0.259	0.129
Depth of 10°C isotherm at 36–39°N	0.301	0.141	0.349
Sea level anomaly	0.296	–0.214	0.296
Upwelling index at 42°N	–0.321	–0.135	–0.024
Upwelling index at 39°N	–0.271	0.357	0.035
Upwelling index at 36°N	–0.148	0.524	0.238
Atmospheric pressure index	0.109	0.498	-0.239

[3] MacFarlane, R. B. 1994. Tiburon Laboratory, NMFS, 3150 Paradise Dr., Tiburon, CA. Personal commun.

that otoliths collected from fish sampled from southern California to British Columbia show distinct growth patterns, indicating little large-scale movement.

One of the best applications of the anomalous 1983 annulus is its use as a chronological marker to improve the accuracy of assigned ages, thus increasing the veracity of age-structured models used in stock assessments (MacLellan and Saunders, 1995). Although the narrow 1983 annuli was most pronounced on young fish at the time of the event, the ring was easily discerned from older fish when their otoliths were broken, burnt, and viewed with reflected light. Therefore, it could be used for decades to aid in the accurate determination of ages of fish born prior to 1983 (Boehlert et al., 1989).

Although the poor environmental conditions present during 1983 appeared to have detrimental effects on the growth of widow and yellowtail rockfish, the effects were short-lived as noted in the increased otolith growth the following years, especially for yellowtail rockfish. As these fish are long-lived (for decades), they have the capacity to absorb occasional years of lower productivity without permanent detrimental effects on the population.

Acknowledgments

Above all, thanks must go to Steve Ralston, whose patience and advice have been extremely valuable. Bill Lenarz, Jim Bence, and Alec MacCall provided research direction. Brian Jarvis and Don Pearson supplied the otoliths used in this study. Don Pearson also allowed me the use of his image enhancement equipment. Kenneth Baltz supplied the oceanographic data. I am grateful to Steve Ralston, Mickey Eldridge, Pete Adams, and two anonymous peer reviews for their critiques of earlier drafts of this manuscript.

Literature cited

Adams, P. B.
1987. The diet of widow rockfish *Sebastes entomelas* in northern California. *In* W. H. Lenarz and D. R. Gunderson (eds.), Widow rockfish: proceedings of a workshop, Tiburon, California, December 11–12, 1980, p. 37–41. U.S. Dep. Commer., NOAA Tech. Rep. NMFS-48.

Bakun, A.
1975. Daily and weekly upwelling indices, west coast of North America, 1967–1973. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-693, 114 p.

Beamish, R. J., and D. R. Bouillon.
1993. Pacific salmon production trends in relation to climate. Can. J. Fish. Aquat. Sci. 50:1002–1016.

Boehlert, G. W., M. M. Yoklavich, and D. B. Chelton.
1989. Time series of growth in the genus *Sebastes* from the northeast Pacific Ocean. Fish. Bull. 87:791–806.

Brodeur, R. D., and W. G. Pearcy.
1984. Food habits and dietary overlap of some shelf rockfishes (genus *Sebastes*) from the northeastern Pacific Ocean. Fish. Bull. 82:269–293.

Cane, M. A.
1983. Oceanographic events during El Niño. Science (Wash. D.C.) 222:1189–1210.

Carlson, H. R., and R. E. Haight.
1972. Evidence for a home site and homing of adult yellowtail rockfish, *Sebastes flavidus*. J. Fish. Res. Board Can. 29:1011–1014.

Casselman, J. M.
1990. Growth and relative size of calcified structures of fish. Trans. Am. Fish. Soc. 119:673–688.

Cushing, D. H.
1975. Marine ecology and fisheries. Cambridge Univ. Press, Cambridge, 278 p.

Dorn, M. W.
1992. Detecting environmental covariates of Pacific whiting *Merluccius productus* growth using a growth-increment model. Fish. Bull. 90:260–278.

Francis, M. P., M. W. Williams, A. C. Pryce, S. Pollard, and S.G. Scott.
1993. Uncoupling of otolith and somatic growth in *Pagrus auratus* (Sparidae). Fish. Bull. 91:159–164.

Germann, I.
1988. Effects of the 1983-El Niño on growth and carbon and nitrogen metabolism of *Pleurophycus gardneri* (Phaeopyceae: Laminariales) in the northeastern Pacific. Mar. Biol. 99:445–455.

Glynn, P. W.
1988. El Niño-Southern Oscillation 1982–1983: nearshore population, community, and ecosystem responses. Annual Review of Ecology and Systematics 19:309–345.

Gunderson, D. R., and T. M. Sample.
1980. Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. Mar. Fish. Rev. 42:2–16.

Lenarz, W. H., and T. Wyllie Echeverria.
1986. Comparison of visceral fat and gonadal fat volumes of yellowtail rockfish, *Sebastes flavidus*, during a normal year and a year of El Niño conditions. Fish. Bull. 84:743–745.

Lombarte, A., and J. Lleonart.
1993. Otolith size changes related with body growth, habitat depth and temperature. Environ. Biol. Fishes 37:297–306.

Lorz, H. V., W. G. Pearcy, and M. Fraidenburg.
1983. Notes on the feeding habits of the yellowtail rockfish, *Sebastes flavidus*, off Washington and in Queen Charlotte Sound. Calif. Fish Game 69:33–38.

MacLellan, S. E., and M. W. Saunders.
1995. A natural tag on the otoliths of Pacific hake (*Merluccius productus*) with implications for age validation and migration. *In* D. H. Secor, J. M. Dean, and S. E. Campana (eds.), Recent developments in fish otolith research, p. 567–580. The Belle W. Baruch Library in Marine Science No. 19. Univ. South Carolina Press, Columbia, SC.

Noakes, D. J., and A. Cambell.
1992. Use of geoduck clams to indicate changes in the marine environment of Ladysmith Harbour, British Columbia. Environmetrics 3:81–97.

Pearcy, W. G.
1992. Movements of acoustically-tagged yellowtail rockfish *Sebastes flavidus* on Heceta Bank, Oregon. Fish. Bull. 90:726–735.

Pearcy, W. G., and A. Schoener.
1987. Changes in the marine biota coincident with the 1982–83 El Niño in the northeast subarctic Pacific Ocean. J. Geophys. Res. 92(C):14417–14428.

Pearson, D. E., and J. E. Hightower.
1991. Spatial and temporal variability in growth of widow rockfish (*Sebastes entomelas*). U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-167, 43 p.

Pereyra, W. T., W. G. Pearcy, and F. E. Carvey Jr.
1969. *Sebastodes flavidus*, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. J. Fish. Res. Board Canada 26:2211–2215.

Rasmusson, E. M.
1984. El Niño: the ocean/atmospheric connection. Oceanus 27(2):5–12.

SAS Institute, Inc.
1988. SAS/STAT user's guide, release 6.03 edition. SAS Institute, Inc., Cary, NC, 1028 p.

Sharp, G. D., and D. R. McClain.
1993. Fisheries, El Niño-Southern oscillation and upper-ocean temperature records: an eastern Pacific example. Oceanography 6:13–22.

Spratt, J. D.
1987. Variation in the growth rate of Pacific herring from San Francisco Bay, California. Calif. Fish Game 73(3): 132–138.

Stanley, R. D., B. M. Leaman, L. Haldorson, and V. M. O'Connell.
1994. Movements of tagged adult yellowtail rockfish, *Sebastes flavidus*, off the west coast of North America. Fish. Bull. 92:655–663.

Strub, P. T., J. S. Allen, A. Huyer, and R. L. Smith.
1987. Large-scale structure of the spring transition in the coastal ocean off western North America. J. Geophys. Res. 92(C2):1527–1544.

VenTresca, D. A., R. H. Parrish, J. L. Houk, M. L. Gingas, S. D. Short, and N. L. Crane.
1995. El Niño effects on the somatic and reproductive condition of blue rockfish, *Sebastes mystinus*. Calif. Coop. Oceanic Fish. Invest. Report 36:167–174.

Weisburg, S.
1993. Using hard-part increment data to estimate age and environmental effects. Can. J. Fish. Aquat. Sci. 50:1229–1237.

Woodbury, D., and S. Ralston.
1991. Interannual variation in growth rates and back-calculated birthdate distributions of pelagic juvenile rockfish (*Sebastes* spp.) off the central California coast. Fish. Bull. 89:523–533.

Wyllie Echeverria, T.
1987. Thirty-four species of California rockfishes: maturity and seasonality of reproduction. Fish. Bull. 85(2): 229–250.

Zimmerman, R. C., and D. L. Robertson.
1985. Effects of El Niño on local hydrography and growth of the giant kelp *Macrocystis pyrifera*, at Santa Catalina Island, California. Limnol. Oceanogr. 30:1298–1302.

General age- and time-dependent growth models for animals

Yongshun Xiao

CSIRO Division of Fisheries
GPO Box 1538, Hobart, Tasmania 7001, Australia
Present address: SARDI Aquatic Sciences Centre
2 Hamra Avenue
West Beach, SA 5024, Australia
E-mail address: xiao.yongshun@pi.sa.gov.au

Abstract.– Most growth models are age-dependent only. Although their modifications can be used to consider, implicitly, the seasonal growth of animals and the effects of tagging, a general framework is unavailable for explicitly incorporating time and time-dependent factors (i.e. ambient temperature and food availability) in age-dependent growth models. In this paper, I derived general age- and time-dependent growth models for animals and gave a comprehensive list of special cases for age- and time-dependent growth models of von Bertalanffy, logistic, and Gompertz types. Such models explicitly incorporate age, time, and their dependent factors and are useful for modeling growth at age and time (e.g. from length-at-age data), incremental growth at age and time increments (e.g. length increments at age and time increments data from tagging studies), the effects of tagging, and the effects of many population characteristics. I also examined their data requirements, their independence of the start of time and adjustment of estimates of parameters essential for ensuing applications, and concluded that age- and time-dependent growth models are useful for subsequent applications, if and only if they are independent of the start of time or time-homogeneous and if estimates of their parameters are properly adjusted. A scheme for such an adjustment is proposed and demonstrated. Finally, I used nine special cases of these general models to analyze tagging data on a centropomid perch (*Lates calcarifer* (Bloch)). Such analyses suggested that tagging is antagonistic to fish growth and leads to a shrinkage of size and that *L. calcarifer* exhibits a strong seasonality in growth, namely its length grows fastest at the start of autumn, grows less until a full stop in the middle of winter, shrinks until the middle of spring, and resumes a positive growth for another cycle.

Manuscript accepted 11 August 1998.
Fish. Bull. 97:690–701 (1999).

Most growth models relate an animal's size to its age alone, are independent of time, and are meant to be useful at all times. Some factors (e.g. ambient temperature and food availability) that are known to affect the growth of animals vary with time, however. Consequently, time has been incorporated in age-dependent growth models implicitly, to consider seasonal (Pitcher and Macdonald, 1973; Appeldoorn, 1987; Smith and McFarlane, 1990; Pauly et al., 1992; Pauly and Gaschütz[1]) and biphasic (Soriano et al., 1992) growth of animals, and the effects of tagging (Xiao, 1994). Xiao's (1996, equations 3.0–4.2, p. 1676–1677) deterministic extensions of the classical von Bertalanffy (1938), logistic (Verhulst, 1838), and Gompertz (1825) growth models also serve these purposes. Similarly, Wang (1998) derived a set of age- and time-dependent growth models for a special case of the von Bertalanffy (1938) growth equation and even constructed distribution-free and consistent estimating functions for estimating their parameters. Although these implicit age- and time-dependent growth models can describe a set of data better than age-dependent growth models, a general framework is unavailable for an explicit incorporation of time and time-dependent factors.

However, an explicit entry of age, time, and time-dependent factors into growth models is essential for studying the effects of many characteristics of a population (e.g. its age composition, size composition, density, and size- or age-specific mortalities) on the growth of its individuals (Moulton et al., 1992; Walker et al., 1998). Indeed, much insight can be gained by examining density-dependent growth alone. This is because density-dependent growth can be effected by 1) compensatory decreases in natural mortality, which may result from a decrease in predation, cannibalism, competition or diseases; 2) compensatory increases in fecundity when food is more readily available or fetal mortality decreases; and 3) compensatory increases in growth rate when more food induces earlier maturity and greater fecundity for each age class (Holden, 1973). For these studies to be feasible, equations for the sizes of individual animals at age a at time t in a population must be coupled with those of their numbers at age a (or size) at time t.

Just as an increase in dimension can reveal new horizons, an explicit incorporation of time and time-dependent factors in age-dependent growth models can be of great use and promise. It also poses interesting philosophical and practical problems. Indeed, in general, time-dependency makes age- and time-

[1] Pauly, D., and G. Gaschütz. 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculators. ICES Council Meeting 1979/G:24, 26 p.

dependent growth models depend on the start of time and thereby renders them useless, unless the start of time is known. Of course, the start of time (if it did start at all) is unknown (although some may settle for the Big Bang) and remains a subject of philosophical debate. It is obvious, then, that, for practical purposes, workable age- and time-dependent growth models must be independent of the start of time. But, under what conditions are they so? How should estimates of their parameters be adjusted to make these models useful for subsequent applications at all times? To answer these questions, both age and time must enter a growth equation, explicitly.

In this paper, I derive general age- and time-dependent growth models for animals and give a comprehensive list of special cases for age- and time-dependent von Bertalanffy (1938), logistic (Verhulst, 1838), and Gompertz (1825) growth models. Such models explicitly incorporate age, time, and their dependent factors and are useful for modeling growth at age and time (e.g. from length-at-age data), incremental growth at age and time increments (e.g. from length increments at age and time increments from tagging studies), the effects of tagging, and the effects of population characteristics. I also examine their data requirements, their independence of the start of time, and adjustment of estimates of their parameters for ensuing applications. Finally, I use nine special cases of these general models to analyze data on length increments at age and time increments from a tagging study of a centropomid perch (*Lates calcarifer* (Bloch)) in the Northern Territory, Australia.

General age- and time-dependent growth models

Just as a formal derivation of age-dependent growth models necessitates use of ordinary differential equations, a formal derivation of age- and time-dependent growth models entails use of partial differential equations. This is because both age and time must be taken into explicit account. Readers unfamiliar with first order partial differential equations may wish to skip immediately to Equations 6–6.3, 10–10.3, and 14–14.3, with little loss of comprehension.

Now, let $0 \le y(a,t) < \infty$, $-\infty < a_0 \le a < \infty$, $0 \le t_0 \le t < \infty$, denote the size of an individual of a species of animal of age a at time t, with an arbitrary reference age a_0 and an arbitrary reference time t_0. Suppose that the change in its size at age a at time t in a small time interval of length Δt is proportional to a function of $y(a,t)$ and Δt, such that

$$y(a + \Delta a, t + \Delta t) - y(a,t) = K(a,t) f(y(a,t)) \Delta t,$$

where $K(a,t)$ is its instantaneous rate of growth in size at age a and time t, and can capture the effects of age, time, and their dependent factors. Dividing both sides of this equation by Δt, Taylor series expansion of $y(a+\Delta a, t+\Delta t)$ in the neighbourhood of (a,t) as

$$y(a + \Delta a, t + \Delta t) = y(a,t) + \frac{\partial y(a,t)}{\partial a} \Delta a + \frac{\partial y(a,t)}{\partial t} \Delta t + O(\Delta t),$$

passing to the limit $\Delta t \to 0$, assuming that

$$\lim_{\Delta t \to 0} O(\Delta t) \to 0,$$

and assuming further that

$$\frac{da}{dt} = 1,$$

yield a first order partial differential equation

$$\frac{\partial y(a,t)}{\partial a} + \frac{\partial y(a,t)}{\partial t} = K(a,t) f(y(a,t)). \tag{1}$$

To solve this equation, I use the following approach. Suppose that the solution of $y(a,t)$ is known. Let $a = t + c$, or $c = a - t$, then

$$w_c(t) = y(t+c, t) \qquad t \ge t_c = \max(t_0, a_0 - c)$$

for a fixed value of $c \in R$. Because $y(a,t)$ satisfies Equation 1, we obtain

$$\frac{dw_c(t)}{dt} = K(t+c,t)f\big(w_c(t)\big). \qquad t \geq t_c \tag{2}$$

Equations 1 and 2 are too general to be solved analytically. Now, I examined three of their special cases for $f(y(a,t))$. For each of these special cases, Table 1 describes where to find equations corresponding to various quantities of interest, and Table 2 describes where to find equations corresponding to various special cases of the solution for $y(a,t)$.

Age- and time-dependent growth models of von Bertalanffy (1938) type I

If $f(y(a,t))=y_{max}(a,t)-y(a,t)$, Equations 1 and 2 become, respectively,

$$\frac{\partial y(a,t)}{\partial a} + \frac{\partial y(a,t)}{\partial t} = K(a,t)\big[y_{\max}(a,t) - y(a,t)\big] \tag{3}$$

$$\frac{dw_c(t)}{dt} = K(t+c,t)\big[y_{\max}(t+c,t) - w_c(t)\big]. \qquad t \geq t_c \tag{4}$$

Of its many interpretations, $y_{max}(a,t)$ can represent the asymptotic size of an average individual as age approaches infinity.

Solution of Equation 4 as an initial value problem with $w_c(t)\,|_{t=t_c} = w_c(t_c)$ yields

$$w_c(t) = w_c(t_c)e^{-\int_{t_c}^{t} K(s+c,s)ds} + \int_{t_c}^{t} K(s+c,s)y_{\max}(s+c,s)e^{-\int_{s}^{t} K(\xi+c,\xi)d\xi} ds. \qquad t \geq t_c \tag{5}$$

If $a-a_0<t$, then $c<0$, $-c>0$, then $t_c=a_0-c=t-a+a_0$; if $a-a_0 \geq t$, then $c \geq 0$, $-c \leq 0$, then $t_c=t_0$. In other words,

$$y(a,t) = \begin{cases} y(a_0, t-a+a_0)e^{-\int_{a-a_0}^{t} K(s+a-t,s)ds} + \int_{t-a+a_0}^{t} K(s+a-t,s)y_{\max}(s+a-t,s)e^{-\int_{s}^{t} K(\xi+a-t,\xi)d\xi} ds & a-a_0 < t \\ y(t_0+a-t,t_0)e^{-\int_{t_0}^{t} K(s+a-t,s)ds} + \int_{t_0}^{t} K(s+a-t,s)y_{\max}(s+a-t,s)e^{-\int_{s}^{t} K(\xi+a-t,\xi)d\xi} ds. & a-a_0 \geq t \end{cases} \tag{6}$$

If $y_{max}(s+a-t,s)=y_{max}$=constant in Equation 6, then

Table 1

Equations corresponding to various quantities of interest for von Bertalanffy (type I) (VB type I), von Bertalanffy (type II) (VB type II), and Gompertz growth equations.

Quantity	VB type I	VB type II	Gompertz
Partial derivative of $y(a,t)$	Equation 3	Equation 7	Equation 11
Derivative of $w_c(t)$	Equation 4	Equation 8	Equation 12
Solution for $w_c(t)$	Equation 5	Equation 9	Equation 13
Solution for $y(a,t)$	Equation 6	Equation 10	Equation 14

Table 2

Equations corresponding to various special cases of the solution for $y(a,t)$ for von Bertalanffy (type I) (VB type I), von Bertalanffy (type II) (VB type II), and Gompertz growth equations.

Assumption about $y_{max}(a,t)$	Assumption about $K(a,t)$	VB type I	VB type	II Gompertz
none	none	6	10	14
$y_{max}(a,t)$=constant	none	6.0	10.0	14.0
$y_{max}(a,t)$=constant	$K(a,t)$=constant	6.1	10.1	14.1
$y_{max}(a,t)$=constant	$K(a,t) = K_0 + A\cos\frac{2\pi}{T}(t-t_\phi)$	6.2	10.2	14.2
$y_{max}(a,t)$=constant	$K(a,t)=K_{max}-(K_{max}-K_{min})e^{-(a-a_0)/\alpha}$ if $a-a_0<t$; $K(a,t)=K_{max}-(K_{max}-K_{min})e^{-(t-t_0)/\alpha}$ if $a-a_0\geq t$	6.3	10.3	14.3

$$y(a,t) = \begin{cases} y_{\max} - \left[y_{\max} - y(a_0, t-a+a_0)\right] e^{-\int_{t-a+a_0}^{t} K(s+a-t,s)\,ds} & a-a_0 < t \\ y_{\max} - \left[y_{\max} - y(t_0+a-t, t_0)\right] e^{-\int_{t_0}^{t} K(s+a-t,s)\,ds} & a-a_0 \geq t \end{cases} \quad (6.0)$$

If $K(s+a-t,s)=K_0$=constant in equation 6.0, then

$$y(a,t) = \begin{cases} y_{\max} - \left[y_{\max} - y(a_0, t-a+a_0)\right] e^{-K_0(a-a_0)} & a-a_0 < t \\ y_{\max} - \left[y_{\max} - y(t_0+a-t, t_0)\right] e^{-K_0(t-t_0)} & a-a_0 \geq t \end{cases} \quad (6.1)$$

which is the age- and time-dependent von Bertalanffy (1938) growth model, or (if $a-a_0$ or $t-t_0$ is interpreted as time at liberty) Fabens (1965) growth model, with parameters K_0 and y_{max}.

Since many factors (e.g. ambient water temperature and food availability) vary seasonally, the instantaneous rate of growth of many animals $K(a,t)$ fluctuates seasonally. If data are available on $K(a,t)$ as a function of these factors, their relationships can be hypothesized. In reality, however, few such data are available. Nonetheless, one can still hypothesize about a temporal trend in $K(a,t)$ and attribute it to the combined effects of all responsible factors. For example, as a first approximation, $K(a,t)$ is seasonal because of seasonal changes in ambient water temperature and food availability and can be approximated by a sine or cosine curve. Thus, if

$$K(s+a-t,s) = K_0 + A\cos\frac{2\pi}{T}(s-t_\phi)$$

in Equation 6.0, an application of the trigonometric function-difference relation

$$\sin(\alpha) - \sin(\beta) = 2\cos\left(\frac{1}{2}(\alpha+\beta)\right)\sin\left(\frac{1}{2}(\alpha-\beta)\right)$$

gives

$$y(a,t) = \begin{cases} y_{\max} - \left[y_{\max} - y(a_0, t-a+a_0)\right] e^{-K_0(a-a_0) - \frac{AT}{\pi}\sin\frac{\pi}{T}(a-a_0)\cos\frac{2\pi}{T}\left(t-t_\phi-\frac{1}{2}(a-a_0)\right)} & a-a_0 < t \\ y_{\max} - \left[y_{\max} - y(t_0+a-t, t_0)\right] e^{-K_0(t-t_0) - \frac{AT}{\pi}\sin\frac{\pi}{T}(t-t_0)\cos\frac{2\pi}{T}\left(t-t_\phi-\frac{1}{2}(t-t_0)\right)}, & a-a_0 \geq t \end{cases} \quad (6.2)$$

where K_0, y_{max}, A, T, and t_ϕ are model parameters to be estimated or specified.

Many species of animals are tagged for a variety of purposes. Tagging can affect the growth of some animals positively, neutrally, or negatively. Indeed, some animals may slow down their growth, cease their growth, or even shrink in size after tagging. A proper functional form of $K(a,t)$ is needed to infer these consequences of tagging. If $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t+a-a_0)/\alpha}$ if $a-a_0<t$ and $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t_0)/\alpha}$ if $a-a_0\geq t$ in Equation 6.0, then (note that $t-a+a_0-t_0=0$, or $t-t_0=a-a_0$)

$$y(a,t)=\begin{cases}y_{\max}-\left[y_{\max}-y(a_0,t-a+a_0)\right]e^{-K_{\max}(a-a_0)-\alpha(K_{\max}-K_{\min})\left[e^{-(a-a_0)/\alpha}-1\right]} & a-a_0<t\\ y_{\max}-\left[y_{\max}-y(t_0+a-t,t_0)\right]e^{-K_{\max}(t-t_0)-\alpha(K_{\max}-K_{\min})\left[e^{-(t-t_0)/\alpha}-1\right]}, & a-a_0\geq t\end{cases} \tag{6.3}$$

where K_{max}, K_{min}, y_{max}, and α are model parameters to be estimated or specified. Clearly, the functional form of $K(a,t)$ serves its purpose well. This is because $K_{max}<K_{min}$, $K_{max}=K_{min}$, and $K_{max}>K_{min}$ indicate, respectively, positive, no, and negative effects of tagging on the growth of animals; and $K_{min}<0$, $K_{min}=0$, and $K_{min}>0$ suggest, respectively, a shrinkage, cessation of growth, and a slower growth of tagged animals immediately after tagging.

Age- and time-dependent growth models of von Bertalanffy (1938) type II

If

$$f(y(a,t))=\frac{y(a,t)}{p}\left[1-\left(\frac{y(a,t)}{y_{\max}(a,t)}\right)^p\right],$$

Equations 1 and 2 become, respectively,

$$\frac{\partial y(a,t)}{\partial a}+\frac{\partial y(a,t)}{\partial t}=K(a,t)\frac{y(a,t)}{p}\left[1-\left(\frac{y(a,t)}{y_{\max}(a,t)}\right)^p\right] \tag{7}$$

$$\frac{dw_c(t)}{dt}=K(t+c,t)\frac{w_c(t)}{p}\left[1-\left(\frac{w_c(t)}{y_{\max}(t+c,t)}\right)^p\right]. \qquad t\geq t_c \tag{8}$$

Solution of Equation 8 (a Bernoulli's equation) as an initial value problem with $w_c(t)\,|_{t=t_c}=w_c(t_c)$ yields

$$w_c(t)=\left[\frac{1}{w_c(t_c)^p}e^{-\int_{t_c}^{t}K(s+c,s)ds}+\int_{t_c}^{t}\frac{K(s+c,s)}{y_{\max}(s+c,s)^p}e^{-\int_{s}^{t}K(\xi+c,\xi)d\xi}ds\right]^{-1/p}. \qquad t\geq t_c \tag{9}$$

If $a-a_0<t$, then $c<0$, $-c>0$, then $t_c=a_0-c=t-a+a_0$; if $a-a_0\geq t$, then $c\geq 0$, $-c\leq 0$, then $t_c=t_0$. In other words,

$$y(a,t)=\begin{cases}\left[\dfrac{1}{y(a_0,t-a+a_0)^p}e^{-\int_{t-a+a_0}^{t}K(s+a-t,s)ds}+\displaystyle\int_{t-a+a_0}^{t}\frac{K(s+a-t,s)}{y_{\max}(s+a-t,s)^p}e^{-\int_{s}^{t}K(\xi+a-t,\xi)d\xi}ds\right]^{-1/p} & a-a_0<t\\ \left[\dfrac{1}{y(t_0+a-t,t_0)^p}e^{-\int_{t_0}^{t}K(s+a-t,s)ds}+\displaystyle\int_{t_0}^{t}\frac{K(s+a-t,s)}{y_{\max}(s+a-t,s)^p}e^{-\int_{s}^{t}K(\xi+a-t,\xi)d\xi}ds\right]^{-1/p}. & a-a_0\geq t\end{cases} \tag{10}$$

If $p=1$, Equations 7–10 and their special cases are reduced to age- and time-dependent growth models of logistic (Verhulst, 1838) type.

If $y_{max}(s+a-t,s)=y_{max}$=constant in Equation 10, then

$$y(a,t)=\begin{cases}\left[\dfrac{1}{y_{\max}^p}-\left(\dfrac{1}{y_{\max}^p}-\dfrac{1}{y(a_0,t-a+a_0)^p}\right)e^{-\int_{t-a+a_0}^{t}K(s+a-t,s)ds}\right]^{-1/p} & a-a_0<t\\ \left[\dfrac{1}{y_{\max}^p}-\left(\dfrac{1}{y_{\max}^p}-\dfrac{1}{y(t_0+a-t,t_0)^p}\right)e^{-\int_{t_0}^{t}K(s+a-t,s)ds}\right]^{-1/p}. & a-a_0\geq t\end{cases} \tag{10.0}$$

If $K(s+a-t,s)$=K_0=constant in Equation 10.0, then

$$y(a,t)=\begin{cases}\left[\dfrac{1}{y_{\max}^{p}}-\left(\dfrac{1}{y_{\max}^{p}}-\dfrac{1}{y(a_0,t-a+a_0)^{p}}\right)e^{-K_0(a-a_0)}\right]^{-1/p} & a-a_0<t\\ \left[\dfrac{1}{y_{\max}^{p}}-\left(\dfrac{1}{y_{\max}^{p}}-\dfrac{1}{y(t_0+a-t,t_0)^{p}}\right)e^{-K_0(t-t_0)}\right]^{-1/p} & a-a_0\geq t\end{cases} \tag{10.1}$$

with parameters K_0 and y_{max}.

If

$$K(s+a-t,s)=K_0+A\cos\frac{2\pi}{T}(s-t_\phi)$$

in Equation 10.0, then

$$y(a,t)=\begin{cases}\left[\dfrac{1}{y_{\max}^{p}}-\left(\dfrac{1}{y_{\max}^{p}}-\dfrac{1}{y(a_0,t-a+a_0)^{p}}\right)e^{-K_0(a-a_0)-\frac{AT}{\pi}\sin\frac{\pi}{T}(a-a_0)\cos\frac{2\pi}{T}\left(t-t_\phi-\frac{1}{2}(a-a_0)\right)}\right]^{-1/p} & a-a_0<t\\ \left[\dfrac{1}{y_{\max}^{p}}-\left(\dfrac{1}{y_{\max}^{p}}-\dfrac{1}{y(t_0+a-t,t_0)^{p}}\right)e^{-K_0(t-t_0)-\frac{AT}{\pi}\sin\frac{\pi}{T}(t-t_0)\cos\frac{2\pi}{T}\left(t-t_\phi-\frac{1}{2}(t-t_0)\right)}\right]^{-1/p}, & a-a_0\geq t\end{cases} \tag{10.2}$$

where K_0, y_{max}, A, T, and t_ϕ are model parameters to be estimated or specified.

If $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t+a-a_0)/\alpha}$, if $a-a_0<t$ and $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t_0)/\alpha}$, if $a-a_0\geq t$ in Equation 10.0, then (note that $t-a+a_0-t_0=0$, or $t-t_0=a-a_0$)

$$y(a,t)=\begin{cases}\left[\dfrac{1}{y_{\max}^{p}}-\left(\dfrac{1}{y_{\max}^{p}}-\dfrac{1}{y(a_0,t-a+a_0)^{p}}\right)e^{-K_{\max}(a-a_0)-\alpha(K_{\max}-K_{\min})\left(e^{-(a-a_0)/\alpha}-1\right)}\right]^{-1/p} & a-a_0<t\\ \left[\dfrac{1}{y_{\max}^{p}}-\left(\dfrac{1}{y_{\max}^{p}}-\dfrac{1}{y(t_0+a-t,t_0)^{p}}\right)e^{-K_{\max}(t-t_0)-\alpha(K_{\max}-K_{\min})\left(e^{-(t-t_0)/\alpha}-1\right)}\right]^{-1/p}, & a-a_0\geq t\end{cases} \tag{10.3}$$

where K_{max}, K_{min}, y_{max}, and α are model parameters to be estimated or specified.

Age- and time-dependent growth models of Gompertz (1825) type

If

$$f(y(a,t))=\lim_{p\to 0}\frac{y(a,t)}{p}\left[1-\left(\frac{y(a,t)}{y_{\max}(a,t)}\right)^{p}\right]=y(a,t)\left[\log_e\left(y_{\max}(a,t)\right)-\log_e\left(y(a,t)\right)\right],$$

Equations 1 and 2 become, respectively,

$$\frac{\partial y(a,t)}{\partial a}+\frac{\partial y(a,t)}{\partial t}=K(a,t)y(a,t)\left[\log_e\left(y_{\max}(a,t)\right)-\log_e\left(y(a,t)\right)\right] \tag{11}$$

$$\frac{dw_c(t)}{dt}=K(t+c,t)w_c(t)\left[\log_e\left(y_{\max}(t+c,t)\right)-\log_e\left(w_c(t)\right)\right]. \qquad t\geq t_c \tag{12}$$

Notice that Equation 12 can be written as a linear ordinary differential equation for $\log_e(w_c(t))$, i.e. as

$$\frac{d\log_e\left(w_c(t)\right)}{dt}=-K(t+c,t)\log_e\left(w_c(t)\right)+K(t+c,t)\log_e\left(y_{\max}(t+c,t)\right).$$

Thus, to obtain equations under the assumption corresponding to Equations 7–10.3, one can either take limits of equations 7–10.3 for $p \to 0$ or solve Equation 12 directly. I chose the latter, without resort to applying the L'Hôpital's rule to log-transformed quantities to evaluate these limits. Solution of Equation 12 as an initial value problem with $w_c(t)\,|_{t=t_c} = w_c(t_c)$ yields

$$w_c(t) = w_c(t_c)\, e^{-\int_{t_c}^{t} K(s+c,s)\,ds} \; e^{\int_{t_c}^{t} K(s+c,s)\log_e(y_{\max}(s+c,s))\, e^{-\int_{s}^{t} K(z+c,s)\,dz}\,ds}, \qquad t \geq t_c \tag{13}$$

If $a-a_0<t$, then $c<0$, $-c>0$, then $t_c=a_0-c=t-a+a_0$; if $a-a_0 \geq t$, then $c \geq 0$, $-c \leq 0$, then $t_c=t_0$. In other words,

$$y(a,t) = \begin{cases} y(a_0, t-a+a_0)\, e^{-\int_{t-a+a_0}^{t} K(s+a-t,s)\,ds} \; e^{\int_{t-a+a_0}^{t} K(s+a-t,s)\log_e(y_{\max}(s+a-t,s))\, e^{-\int_{s}^{t} K(z+a-t,s)\,dz}\,ds}, & a-a_0 < t \\ y(t_0+a-t, t_0)\, e^{-\int_{t_0}^{t} K(s+a-t,s)\,ds} \; e^{\int_{t_0}^{t} K(s+a-t,s)\log_e(y_{\max}(s+a-t,s))\, e^{-\int_{s}^{t} K(z+a-t,s)\,dz}\,ds}, & a-a_0 \geq t \end{cases} \tag{14}$$

If $y_{max}(s+a-t,s)=y_{max}$=constant in Equation 14, then

$$y(a,t) = \begin{cases} y_{\max}\left[\dfrac{y(a_0, t-a+a_0)}{y_{\max}}\right]^{e^{-\int_{t-a+a_0}^{t} K(s+a-t,s)\,ds}}, & a-a_0 < t \\ y_{\max}\left[\dfrac{y(t_0+a-t, t_0)}{y_{\max}}\right]^{e^{-\int_{t_0}^{t} K(s+a-t,s)\,ds}}, & a-a_0 \geq t \end{cases} \tag{14.0}$$

If $K(s+a-t,s)=K_0$=constant in Equation 14.0, then

$$y(a,t) = \begin{cases} y_{\max}\left[\dfrac{y(a_0, t-a+a_0)}{y_{\max}}\right]^{e^{-K_0(t-a+a_0)}}, & a-a_0 < t \\ y_{\max}\left[\dfrac{y(t_0+a-t, t_0)}{y_{\max}}\right]^{e^{-K_0(t-t_0)}}, & a-a_0 \geq t \end{cases} \tag{14.1}$$

which is the age- and time-dependent Gompertz (1825) growth model, with parameters K_0 and y_{max}.

If

$$K(s+a-t,s) = K_0 + A\cos\frac{2\pi}{T}(s-t_\phi)$$

in Equation 14.0, then

$$y(a,t) = \begin{cases} y_{\max}\left[\dfrac{y(a_0, t-a+a_0)}{y_{\max}}\right]^{e^{-K_0(t-a+a_0)-\frac{AT}{\pi}\sin\frac{\pi}{T}(t-a+a_0)\cos\frac{2\pi}{T}\left(t-t_\phi-\frac{1}{2}(t-a+a_0)\right)}}, & a-a_0 < t \\ y_{\max}\left[\dfrac{y(t_0+a-t, t_0)}{y_{\max}}\right]^{e^{-K_0(t-t_0)-\frac{AT}{\pi}\sin\frac{\pi}{T}(t-t_0)\cos\frac{2\pi}{T}\left(t-t_\phi-\frac{1}{2}(t-t_0)\right)}}, & a-a_0 \geq t \end{cases} \tag{14.2}$$

where K_0, y_{max}, A, T, and t_ϕ are model parameters to be estimated or specified.

If $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t+a-a_0)/\alpha}$ if $a-a_0<t$ and $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t_0)/\alpha}$ if $a-a_0\geq t$ in Equation 14.0, then (note that $t-a+a_0-t_0=0$, or $t-t_0=a-a_0$)

$$y(a,t)=\begin{cases} y_{\max}\left[\dfrac{y(a_0,t-a+a_0)}{y_{\max}}\right]^{e^{-K_{\max}(a-a_0)-\alpha\cdot K_{\max}-K_{\min})(e^{-(a-a_0)/\alpha}-1)}} & a-a_0<t \\ y_{\max}\left[\dfrac{y(t_0+a-t,t_0)}{y_{\max}}\right]^{e^{-K_{\max}(t-t_0)-\alpha\cdot K_{\max}-K_{\min})(e^{-(t-t_0)/\alpha}-1)}} & a-a_0\geq t \end{cases} \quad (14.3)$$

where K_{max}, K_{min}, y_{max}, and α are model parameters to be estimated or specified.

Data requirements for parameter estimation

Equations 6, 10, and 14, and their special cases are segmented functions; they provide flexibility in the analysis of growth data. Thus, by appropriately choosing time t (which is a relative quantity), one can use either segment ($a-a_0<t$ or $a-a_0\geq t$) for an individual animal or for a group of individuals, or use both segments ($a-a_0<t$ and $a-a_0\geq t$) for a group of individuals. It is, however, more convenient to use only one segment in a single analysis. Indeed, although growth parameters can be estimated by use of either segment of any of Equations 6.1, 6.2, 6.3; 10.1, 10.2, 10.3; 14.1, 14.2, 14.3, it is easier to use the segment for $a-a_0<t$, by letting time t start before the animals, whose growth is to be modeled, are born, unless time is allowed to take negative values. Use of the other segment, i.e., that for $a-a_0\geq t$, gives identical results, but it is tortuous and requires first calculating $y(t_0+a-t,t_0)$.

Data requirement for estimation of parameters in a growth model is a function of the generality of that model: the more general it is, the more data it generally requires. Equations 6, 6.0, 10, 10.0, 14, and 14.0 generally require knowledge of two ages a_0 and a, time t, and two sizes $y(a_0,t-a+a_0)$ and $y(a,t)$ if $a-a_0<t$; or knowledge of two times t_0 and t, age a, and two sizes $y(t_0+a-t,t_0)$ and $y(a,t)$ if $a-a_0\geq t$.

By contrast, use of Equations 6.1, 10.1, and 14.1 only requires knowledge of the difference between two ages $a-a_0$, and two sizes $y(a_0,t-a+a_0)$ and $y(a,t)$; or of the difference between two times $t-t_0$, and two sizes $y(t_0+a-t,t_0)$ and $y(a,t)$. Equation 6.1 has been widely used to model tagging data, where a_0 or t_0 is interpreted as time at release, a or t as time at recapture, $a-a_0$ or $t-t_0$ as time at liberty, $y(a_0,t-a+a_0)$ or $y(t_0+a-t,t_0)$ as size at release, and $y(a,t)$ as size at recapture. It has also been used extensively to model size at age data (obtained, say, by ageing animals by reading marks in their hard parts), where a_0 or t_0 is interpreted as age at birth, a or t as age, $y(a_0,t-a+a_0)$ or $y(t_0+a-t,t_0)$ as size at birth, and $y(a,t)$ as size at age. However, it is rare to know an animal's two ages and their corresponding sizes; what are commonly measured are one age and its corresponding size. Consequently, it is common practice to fit Equation 6.1 into such size-at-age data to estimate age at birth a_0 or t_0, as well as the growth parameters, thereby implicitly assuming, for all animals concerned, that the size at birth $y(a_0,t-a+a_0)$ or $y(t_0+a-t,t_0)$ is zero and that the age at birth a_0 or t_0 is the same. Exactly the same argument applies to Equations 6.2, 6.3, 10.1, 10.2, 10.3, 14.1, 14.2, and 14.3.

Data analysis

Barramundi *L. calcarifer* is a protandrous fish found in estuaries and other coastal areas of the Indo-West Pacific (Griffin, 1987). Between August 1977 and June 1980, 4933 barramundi with a body total-length range of about 10–100 cm were captured by a combination of lure fishing, tidal trap, seine, and gill net. They were measured to the nearest centimeter, tagged with the then commonly used, but apparently physically and physiologically damaging, Floy FT-2 dart tags for fish >35 cm and FD-67 anchor tags for fish <35 cm, and released in rivers flowing into the Van Diemen Gulf and the Gulf of Carpentaria of northern Australia (Davis and Reid, 1982). Of those tagged, 312 fish of a total length of 23–92 cm (mean=60 cm, SE=13 cm) were recaptured, but only 308 are used in the analysis below owing to incomplete recapture information. The time at liberty ranged from zero to 932 d, with a mean of 219 d (SE=211 d), and the length increment from –21 to 35 cm, with a mean of 6 cm (SE=8 cm). Negative increments in length are often observed in a tagging experiment because tagged animals can shrink in size immediately after tagging.

Let a_0 or t_0 denote time at release, a or t, time at recapture, $a-a_0$ or $t-t_0$, time at liberty, $y(a_0,t-a+a_0)$ or $y(t_0+a-t,t_0)$, the length of a fish at release, $y(a,t)$,

its length at recapture, and y_{max}, its maximum length. The segments of Equations 6.1, 10.1, 14.1; Equations 6.2 (p=1), 10.2 (p=1), 14.2 (p=1); and Equations 6.3, 10.3, 14.3, all for $a-a_0<t$, were fitted into the tagging data, by using the nonlinear least squares method, under the assumptions that T=365.25 d, time started (i.e. time t=0) on 1 January 1960 (see below for its significance), and errors in $y(a,t)$ follow independent normal distributions, with a mean of $\hat{y}(a,t)$ and a constant variance of σ^2 (Table 3). A likelihood ratio test suggests that Equation 6.1 is significantly different from Equation 6.2 ($F_{2,304}$=48.6892, P<0.0001) or from Equation 6.3 ($F_{2,304}$=4.1238, P=0.0171); Equation 10.1 (p=1) is significantly different from Equation 10.2 (p=1) ($F_{2,304}$=45.3460, P<0.0001) or from Equation 10.3 (p=1) ($F_{2,304}$=3.3241, P=0.0373); and Equation 14.1 is significantly different from Equation 14.2 ($F_{2,304}$=46.8516, P<0.0001) or from Equation 14.3 ($F_{2,304}$=3.5345, P=0.0304). Thus, Equations 6.2, 6.3; Equations 10.2 (p=1), 10.3 (p=1); and Equations 14.2, 14.3, and their associated estimates of parameters seem adequate for describing the tagging data. Selection between equations 6.2 and 6.3, between Equations 10.2 and 10.3, and between Equations 14.2 and 14.3 by developing more general models of $K(a,t)$ was not successful because of a lack of data.

Are equations 6.1, 6.2, 6.3; 10.1, 10.2, 10.3; 14.1, 14.2, 14.3 independent of the start of time?

An age- and time-dependent growth model is useful, if and only if it is independent of the start of time or if it is time-homogeneous. The reason for this is that start of time is unknown. For Equations 6.0, 10.0 and 14.0 to be useful,

$$\int_{t-a+a_0}^{t} K(s+a-t,s)ds$$

if $a-a_0<t$ or

$$\int_{t_0}^{t} K(s+a-t,s)ds$$

if $a-a_0 \geq t$ must be independent of the start of time t. Obviously, Equations 6.1, 6.2, 6.3; 10.1, 10.2, 10.3; 14.1, 14.2, and 14.3 all are independent of the start of time, where time t appears as time differences $t-t_0$ or $t-t_\phi$.

However, interesting differences exist among them. Equations 6.1, 6.3, 10.1, 10.3, 14.1, and 14.3 apply on any time scales, without any adjustment of estimates of their parameters in subsequent applications because they depend on time difference $t-t_0$ or age difference $a-a_0$ only. By contrast, Equations 6.2, 10.2 and 14.2 and estimates of their parameters must be properly adjusted for this purpose. Specifically, the estimate of parameter t_ϕ in Equations 6.2, 10.2, and 14.2 must be correctly adjusted before their subsequent applications. To make such an adjustment, suppose that all growth parameters are estimated from tagging data by using one segment of Equation 6.2, 10.2, or 14.2 on one time scale (regression time scale, Fig. 1), with time t, parameter t_ϕ (estimated), and a reference time t_r (known). Now, Equation 6.2, 10.2, or 14.2 is to be applied in a future fish stock assessment on another time scale (application time scale, Fig. 1), with time t', parameter t_ϕ' (unknown,

Table 3

Estimates and (in parentheses) standard errors of parameters by fitting Equations 6.1, 6.2, 6.3; 10.1 (p=1), 10.2 (p=1), 10.3 (p=1); and 14.1, 14.2, 14.3 to the barramundi tagging data using the least squares method under the assumptions that T=365.25 d, time started (i.e. time t=0) on 1 January 1960, and errors in $y(a,t)$ follow independent normal distributions, with a mean of $\hat{y}(a,t)$ and a constant variance of σ^2. P<0.0001; n=308; — = not applicable.

Equation	$\hat{y}_{max}(a,t)$ (cm)	$\hat{K}_0$ or $\hat{K}_{max}$ ($\cdot$d^{-1})	$\hat{A}$ or $\hat{K}_{min}$ ($\cdot$d^{-1})	$\hat{t}_\phi$ or $\hat{\alpha}$ (d)	df_1, df_2, F	$\hat{\sigma}^2$ (cm^2)	R^2
6.1	113.4724 (9.6232)	0.00065 (0.00013)	—	—	2,306,30965.9769	22.8923	0.9951
6.2	114.4452 (8.6686)	0.00061 (0.00011)	0.00088 (0.00018)	62.7197 (06.8279)	4,304,20333.2870	17.4525	0.9963
6.3	110.1152 (8.5316)	0.00078 (0.00017)	–0.00028 (0.00121)	28.7594 (41.6473)	4,304,15801.1643	22.4343	0.9952
10.1	94.7255 (3.2775)	0.00161 (0.00014)	—	—	2,306,30895.5263	22.9443	0.9951
10.2	96.2908 (3.0613)	0.00148 (0.00012)	0.00217 (0.00028)	63.5155 (06.7582)	4,304,19947.8597	17.7884	0.9962
10.3	94.4251 (3.1934)	0.00182 (0.00020)	–0.00012 (0.00250)	37.3267 (63.1348)	4,304,15684.0774	22.6010	0.9952
14.1	100.5592 (4.8653)	0.00114 (0.00014)	—	—	2,306,31051.6220	22.8295	0.9951
14.2	102.1717 (4.5198)	0.00104 (0.00011)	0.00153 (0.00022)	63.2525 (06.7674)	4,304,20202.0707	17.5654	0.9963
14.3	99.6456 (4.6446)	0.00129 (0.00018)	–0.00028 (0.00203)	31.6268 (51.7115)	4,304,15784.7666	22.4575	0.9952

to be calculated), and a reference time t_r' (known). Both reference times must be chosen properly, such that $t_r=t_c$ on t_r's scale and $t_r'=t_c$ on t_r''s scale, where t_c is an arbitrarily chosen time. For example, $t_r=0$ on t_r's scale; $t_r'=0$ on t_r''s scale. Projection of both $t_r=t_c$ on t_r's scale and $t_r'=t_c$ on t_r''s scale onto a third time scale (projection time scale, Fig. 1) to find their time difference on the third time scale $\tau_r'-\tau_r$. It is this time difference that is to be used to calculate t_ϕ'. To do so, let $t_r-t_\phi=t_r'-t_\phi'$, or $t_\phi'=t_\phi+t_r'-t_r=t_\phi+\tau_r'-\tau_r$, $t-t_\phi=t'-t_\phi'=t'-t_\phi-t_r'+t_r=t'-t_\phi-\tau_r'+\tau_r$. Therefore, in Equations 6.2, 10.2, and 14.2, replacement of $t-t_\phi$ with $t'-t_\phi-\tau_r'+\tau_r$, of $a-a_0$ with $a'-a_0'$, and of $t-t_0$ with $t'-t_0'$ will give the correct growth models for the future fish stock assessment on the required time scale (application scale). For the barramundi growth described by equation 6.2, $\hat{t}_\phi$= 62.7197 d, $t_r=0$ corresponds to $\tau_r=1$ January 1960 (row 2, Table 3), $t_r'=0$ corresponds to $\tau_r'=1$ January 1999, then $t_\phi'=\hat{t}_\phi+\tau_r'-t_r$=62.7197+(1 January 1999)–(January 1, 1960)=62.7197+14245=14307.7197 d. Therefore, replacement of $t-t_\phi$ with $t'-14307.7197$, of $a-a_0$ with $a'-a_0'$, and of $t-t_0$ with $t'-t_0'$ in the model concerned will give the correct growth models for the future (when time starts on 1 January 1999) barramundi stock assessment on the required time scale (application scale). In this example, the third time scale (projection time scale) is, of course, calendar time.

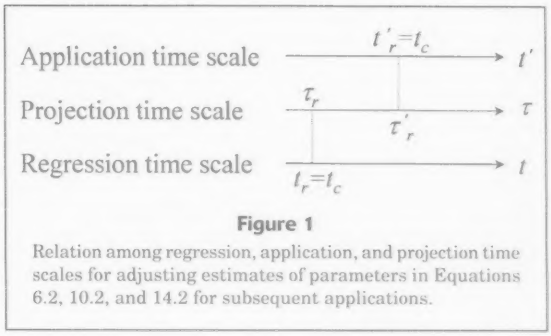


Figure 1

Relation among regression, application, and projection time scales for adjusting estimates of parameters in Equations 6.2, 10.2, and 14.2 for subsequent applications.

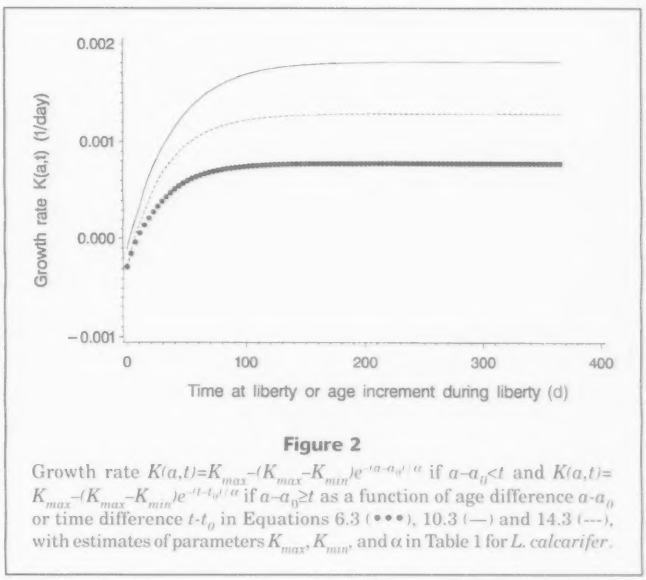


Figure 2

Growth rate $K(a,t)=K_{max}-(K_{max}-K_{min})e^{-(t-t_0)/\alpha}$ if $a-a_0<t$ and $K(a,t)=K_{max}-(K_{max}-K_{min})e^{-(t-t_0)/\alpha}$ if $a-a_0\geq t$ as a function of age difference $a-a_0$ or time difference $t-t_0$ in Equations 6.3 (•••), 10.3 (—) and 14.3 (---), with estimates of parameters K_{max}, K_{min}, and α in Table 1 for *L. calcarifer*.

Discussion

This work presents general age- and time-dependent models for the growth of animals and a comprehensive list of their useful special cases, forming a basis for obtaining quantitative information on the growth of animals experiencing changes in age, time, and age- and time-varying factors. These models have many applications. An obvious one would be to examine both the short- and long-term effects of tagging on the growth of animals by use of Equations 6.3, 10.3, and 14.3; $K_{max}<K_{min}$, $K_{max}=K_{min}$, and $K_{max}>K_{min}$ indicate, respectively, positive, no, and negative effects of tagging on the growth of animals. Similarly, $K_{min}<0$, $K_{min}=0$, and $K_{min}>0$ suggest, respectively, a shrinkage, cessation of growth, and a slower growth of tagged animals immediately after tagging. In the case of the *L. calcarifer* (Fig. 2), tagging seems to have been antagonistic to its growth ($K_{max}>K_{min}$) and led to a shrinkage of its size ($K_{min}<0$). This conclusion is tentative, however, because of the large standard error of $\hat{\alpha}$.

Another application would be to study how age- and time-dependent factors other than age and time affect the growth of animals. For example, one can hypothesize about the functional forms of $K(a,t)$, such as $K(a,t)=\alpha T(t-t_r)^\beta$, where $T(t)$ is ambient temperature, availability of food, or pH value; t_r (a time lag or lead), and α and β are all parameters to be estimated or specified. Such a model is ideal for analyzing data on the length or weight of an individual animal at age and time, which may be available, say, from aquaculture operations. It might also be useful for analyzing data from mark-recapture experiments, where ambient temperature or food availability of a tagged animal is measured continuously from the time of its tagging to the time of its recapture. Indeed, if *L. calcarifer* had been tagged with a "smart" tag that could record ambient temperature or food availability, analysis would have been made of their

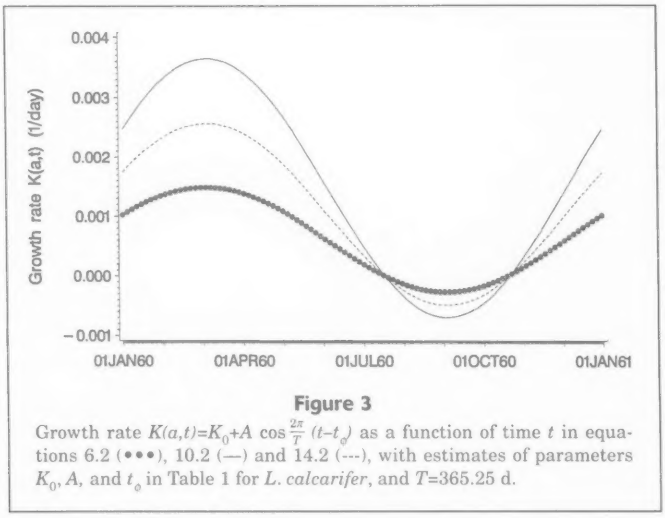


Figure 3

Growth rate $K(a,t)=K_0+A\cos\frac{2\pi}{T}(t-t_\phi)$ as a function of time t in equations 6.2 (•••), 10.2 (—) and 14.2 (---), with estimates of parameters K_0, A, and t_ϕ in Table 1 for *L. calcarifer*, and T=365.25 d.

lengths at release and recapture and at times at liberty in the above application. It should be noted, however, that the information from a tagging experiment is limited. It might not be possible to estimate all the parameters in the model reliably, as in the case of the *L. calcarifer* data. Such a limitation also applies to extracting environmental signals from growth data.

More importantly, all the above models can be used to study the population dynamics of some species of animals, simply by letting $y(a,t)$ denote the number of individuals of a species of animals of age a at time t. Indeed, similar models in studies of population dynamics also lead to partial differential equations (e.g. Nisbet and Gurney, 1982).

It is interesting that *L. calcarifer* is a tropical and subtropical species of fish and yet exhibits a strong seasonal growth. For all three models (Equations 6.2, 10.2, or 14.2), its growth rate $K(a,t)$ reaches its maximum on 3 or 4 March (i.e. at the start of autumn), slows down to zero on 17 July (i.e. in the middle of winter), reaches its minimum on 2 or 3 September (i.e. at the start of spring), returns to zero on 19 or 20 October (i.e. in the middle of spring), and comes back to its maximum rate on 3 or 4 March (i.e. at the start of autumn) (Fig. 3). Thus, its length grows fastest on 3 or 4 March (i.e. at the start of autumn), grows less until a full stop on 17 July (i.e. in the middle of winter), shrinks until 19 or 20 October (i.e. in the middle of spring), and resumes a positive growth for another cycle. Thus, *L. calcarifer* does not grow in length for three months in a year, from 17 July (i.e. in the middle of winter) to 19 or 20 October (i.e. in the middle of spring). Such a strong seasonality in growth seems related to the seasonal availability of food and seasonal changes in water temperature.

Finally, notice my use of the length at recapture rather than length increment of a tagged individual as the independent variable in relevant models and in the data analysis. This was to avoid error propagation. The variance of the length increment is

$$V(L_2-L_1)=V(L_2)+V(L_1)-2\rho(L_1,L_2)\sqrt{V(L_1)V(L_2)},$$

where $\rho(L_1,L_2)$ is the correlation coefficient between lengths L_1 and L_2.

A higher value of noise to signal ratio is expected if length increments are used; the higher value of noise to signal ratio helps mask patterns in the data and makes their analysis difficult.

Acknowledgments

I am most grateful to Grant G. Thompson (Alaska Fisheries Science Center, NMFS) and an anonymous referee for their valuable comments on this work that have substantially improved its presentation and for their encouragement. I also wish to thank You-Gan Wang (CSIRO IPP&P Biometrics Unit) for stimulating discussions; Yong Chen (Memorial University), Tony Fowler (SARDI Aquatic Sciences Centre), Charlie Macaskill (School of Mathematics and Statistics, University of Sydney) for commenting on an earlier version of the manuscript, and Xiaoxu Li (SARDI Aquatic Sciences Centre) for producing Figure 1. Roland K. Griffin (Northern Territory Department of Primary Industry and Fisheries) and Tim L. O. Davis (CSIRO Division of Fisheries) kindly supplied the *Lates calcarifer* data. John D. Stevens and Anthony D. M. Smith (CSIRO Division of Fisheries) are thanked for supervising this project. The work was funded by the Australian Fisheries Management Authority.

Literature cited

Appeldoorn, R. S.
1987. Modification of a seasonally oscillating growth function for use with mark-recapture data. J. Cons. Int. Explor. Mer 43:194–198.

Davis, T. L. O., and D. D. Reid.
1982. Estimates of tag shedding rates for Floy FT-2 dart and FD-67 anchor tags in barramundi, *Lates calcarifer* (Bloch). Aust. J. Mar. Freshwater Res. 33:1113–1117.

Fabens, A. T.
1965. Properties and fitting of von Bertalanffy growth curves. Growth 29:265–289.

Gompertz, B.
1825. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. Philos. Trans. R. Soc. Lond. 115 (1):513–585.

Griffin, R. K.
1987. Life history, distribution, and seasonal migration of barramundi in the Daly River, Northern Territory, Australia. Am. Fish. Soc. Symp. 1:358–363.

Holden, M. J.
1973. Are long-term sustainable fisheries for elasmobranchs possible? Rapp. P.-V. Reun. Cons. Int. Explor. Mer 164:360–367.

Moulton, P. L., T. I. Walker, and S. R. Saddlier.
1992. Age and growth studies of gummy shark, *Mustelus antarcticus* Günther, and school shark, *Galeorhinus galeus* (Linnaeus), from southern Australian waters. Aust. J. Mar. Freshwater Res. 43:1241–1267.

Nisbet, R. M., and W. S. C. Gurney.
1982. Modelling fluctuating populations. Wiley & Sons, New York, NY, 379 p.

Pauly, D., M. Soriano-Bartz, M. J. Moreau, and A. Jarre-Teichmann.
1992. A method accounting for seasonal cessation of growth in fishes. Aust. J. Mar. Freshwater Res. 43:1151–1156.

Pitcher, T. J., and P. D. M. Macdonald.
1973. Two models for seasonal growth in fishes. J. Appl. Ecol. 10:599–606.

Smith, D. S., and G. A. McFarlane.
1990. Growth analysis of Strait of Georgia lingcod by use of length-frequency and length-increment data in combination. Trans. Am. Fish. Soc. 119:802–812.

Soriano, M., J. Moreau, J. M. Hoenig, and D. Pauly.
1992. New functions for the analysis of two-phase growth of juvenile and adult fishes, with application to Nile perch. Trans. Am. Fish. Soc. 121:486–493.

Verhulst, P. F.
1838. Notice sur la loi que la population pursuit dans son accroissement. Corresp. Math. Phy. 10:113–121.

von Bertalanffy, L.
1938. A quantitative theory of organic growth. Hum. Biol. 10:181–213.

Walker, T. I., B. L. Taylor, R. J. Hudson, and J. P. Cottier.
1998. The phenomenon of apparent change of growth rate in gummy shark (*Mustelus antarcticus*) harvested off southern Australia. Fish. Res. 39:139–163.

Wang, Y.-G.
1998. Growth curves with explanatory variables and estimation of the effect of tagging. Aust. N.Z. J. Stat. 40:299–304.

Xiao, Y.
1994. Growth models with corrections for the retardative effects of tagging. Can. J. Fish. Aquat. Sci. 51:263–267.
1996. How does somatic growth rate affect otolith size in fishes? Can. J. Fish. Aquat. Sci. 53:1675–1682.

An analysis of variation in catchability of green tiger prawn, *Penaeus semisulcatus*, in waters off Kuwait

Yimin Ye

Hussain M. A. Mohammed

Mariculture and Fisheries Department
Kuwait Institute for Scientific Research
P. O. Box 1638, 22017 Salmiya, Kuwait
E-mail address (for Y. Ye)): yye@safat.kisr.edu.kw

Abstract.—A method for assessing variation in catchability of single cohort fisheries based on catch and effort statistics was developed. The results of its application to the Kuwait shrimp, *Penaeus semisulcatus*, fishery showed that catchability declined gradually with progress of fishing in general, but there was a rise in December or January. The pattern of variation was associated with possible schooling behavior at the beginning of a fishing season. Initially, catchability was high, but, as intensive fishing dispersed the schools, or reduced population density, catchability declined. The midwinter increase in catchability was probably due to an inshore spawning migration. There were also substantial interseasonal variations in catchability because schooling was associated with strong recruitment and environmental conditions.

Manuscript accepted 25 June 1998.
Fish. Bull. 97:702–712 (1999).

Most fishery management regulations are based on estimation of resource abundance and fishing mortality, of which catchability is an essential element. The existing literature on population dynamics rarely deals directly with catchability *per se*. For most production models and cohort models that use abundance indices, catchability is usually taken as constant and, subsequently, catch per unit of effort (CPUE) from commercial catch and effort statistics is used as an index of stock abundance.

The assumption of constant catchability is rarely, if ever, valid within a fishing season (Garcia, 1988; Atran and Loesch, 1995; Hannah, 1995; Arreguin-Sanchez, 1996), particularly for short-lived species such as certain shrimp in Kuwait's waters. Catchability depends on many factors: sensory capabilities, behavioral response of the target species (Penn, 1984; Wassenberg and Hill, 1990), environmental factors including temperature (Chittelborough, 1970; Morgan, 1974; Hill, 1985) and wind (Ehrich and Groger[1]), stock area, the relative distribution of fish and fishing (Winters and Wheeler, 1985; Hannah, 1995), and stock abundance (MacCall, 1976, 1990; Murphy, 1977; Csirke, 1989). Ricker (1975) stated that variation in catchability is likely to be the greatest source of error in models based on CPUE with constant catchability.

Shrimp fisheries are often managed by a minimum spawning stock strategy to prevent overfishing of stocks. Under such a strategy, CPUE during a spawning season is usually used as an index of spawning stock abundance, and fishing is closed when CPUE falls below a certain level (Penn, 1984; Morgan, 1989). If catchability is highly variable, indices of spawning stocks and the underlying stock recruitment relationship could be obscured and perhaps lead to erroneous management decisions (Hannah, 1995).

Studies on catchability are essential for relating stock abundance to observed CPUE. By investigating within-season changes in catchability, properties of a stock that are not apparent when only annual data are examined, can be understood better. The objective of this paper is to develop a method to estimate changes in catchability from commercial catch and effort data.

Materials and methods

The model

The *Penaeus semisulcatus* fishery in waters off Kuwait has a single major recruitment in June and July,

[1] Ehrich, S., and D. Groger. 1989. Diurnal variation in catchability of several fish species in the North Sea. ICES Council Meeting (CM) 1989/B:35, 10 p.

which, depending on the year, may be supplemented by a second, late-summer recruitment in August or early September (Mohammed et al., 1996). The success of the second recruitment was responsible for record landings, for example, in the 1988–89 and 1989–90 seasons (Siddeek et al., 1994). Total landings of *P. semisulcatus* in 1994–95 and 1995–96 were 699.7 and 925.0 tonnes, respectively, about 14% and 19% of the 1988–89 season's *P. semisulcatus* catch of 5022.4 tonnes (Siddeek et al., 1994).

Kuwait's opening date for shrimping has been set at 1 September since 1987 (Gulland, 1989; Siddeek and Abdul-Ghaffar, 1989). The season is closed when the CPUE for combined species of the industrial fleet falls below 80–120 kg/boat-day (Xu et al., 1995). In this case, shrimp trawling is a process that depletes a single cohort.

We start with three basic equations. The first equation is the relation between fishing mortality and fishing effort:

$$F_t = q_j f_t, \tag{1}$$

where q_j = catchability in month j;
F_t = fishing mortality in time interval t (5 days per interval); and
f_t = fishing effort in time interval t.

The second relates the population number at time t to the initial cohort number and cumulative fishing and natural mortalities:

$$N_t = Re^{-\sum_{i=1}^{t} F_i - tM}, \tag{2}$$

where R = initial stock number;
N_t = population number at time t;
i = time interval; and
M = natural mortality.

The final equation relates catch to current abundance and fishing as well as to natural mortalities, and we assume that fishing mortality acts independently of natural mortality, taking a fraction of $F/(F+M)$ of the total mortality, so

$$C_t = N_t \frac{F}{F_t + M}\left(1 - e^{-(F_t + M)}\right), \tag{3}$$

where C_t = catch in time interval t.

The three equations describe an exponential decay process of a single cohort with fishing and natural mortalitites. Natural morality is assumed to be independent of time throughout the season and catchability is assumed to remain constant within a month.

Given catch and effort data, the initial population number (R), natural mortality rate (M), and six monthly catchability rates (q_j), a total of eight parameters can be estimated in theory by a time-series fitting method of least squares between observed and predicted catches. There exists, however, a problem of confounding the initial stock number, natural mortality, and catchabilities. A high initial population number with high natural mortality and low catchability rates gives as good a fit as does a low initial population number with a low natural mortality and high catchability rates. The following three measures were taken to solve this problem.

1) We assumed that

$$R = \frac{1}{q_1}\sum_{t=1}^{3} C_t' \Big/ \sum_{t=1}^{3} f_t, \tag{4}$$

where C'_t = observed catch at time t.

This assumption says, in effect, that for a given estimate of q_1, we have an estimate of the initial population number (R) from the average catch and effort over the first three time intervals (Hilborn and Walters, 1992). 2) It was presumed that natural mortality was available from other sources. 3) Auxiliary abundance index was used in the time series fitting as follows:

$$SS = \sum_{t=1}^{T}\left[\ln(C_t) - \ln(C_t')\right]^2 + W\sum_{j=1}^{J}\left[\ln(X_j) - \ln(X_j')\right]^2, \tag{5}$$

where C_t = predicted catch at time t by Equation 3;
C_t' = observed catch at time t;
X_j' = observed index of stock number in month j in relation to the beginning point of a fishing season;
X_j = predicted relative stock abundance in the middle of month j, i.e. predicted stock number in month j divided by the predicted stock number of the middle point of the beginning month; and
W = the weight given to the deviation between the predicted and the observed stock indices.

This procedure reduced the number of parameters to be estimated to six. Monthly CPUE of the United Fisheries of Kuwait (UFK) fleet was used as auxiliary information about stock abundance.

The data

The shrimp fishery in Kuwait consists of two sectors: industrial trawlers and dhow trawlers (for a review see Mathews and Samuel, 1991; Mathews, 1994; Ye et al., 1996). The main species caught are *P. semisulcatus*, *Metapenaeus affinis*, and *Parapenaeopsis stylifera*. *Penaeus semisulcatus* dominates in the central and southern waters, and the other two species are mainly distributed in northern waters. The dhow boats trawl in relatively shallow waters, and their catches are auctioned at local fish markets (Abdul-Ghaffar and Al-Ghunaim, 1994; Ye et al., 1996). Species composition of the dhow catch varies with changes in fishing grounds and with seasonal migration. The monthly percentages of *P. semisulcatus* in the dhow landings change greatly within a season, for example, from 29.6 to 87.1% in 1993–94. Owing to the difficulty in collecting reliable effort data from the dhow sector, effort is usually standardized in relation to that of the industrial sector in reporting Kuwait's shrimp fishery statistics. The dhow effort is thus calculated by dividing the total catch of combined species of the dhow sector by the CPUE of combined species from the industry sector (Mathews, 1994), which ignores the change in target species. The catchability of *P. semisulcatus* under such a standardized effort would change simply because of the variation in target species.

The industry sector comprises three companies: United Fisheries of Kuwait (UFK), Bubiyan Fishing Company, and National Fishing Company. The shrimp catch landed by UFK is mainly exported. Fishing operations of the UFK fleet are mainly in the southern and central Kuwait waters, where *P. semisulcatus* dominates (Siddeek et al., 1989); this occurs because *P. semisulcatus* is individually larger and much more valuable in international markets than the other two species (Siddeek et al., 1989; Ye et al., 1996). Consequently, the percentage of *P. semisulcatus* in the UFK catch remains relatively less variable within a season, for example between 59.5% and 84.5% in the 1993–94 season (Ye et al., 1996).

Seasonal landing data from the dhow boats were recorded every five days (Mohammed et al., 1996); however, industrial fleets reported their catches and fishing effort monthly. To estimate monthly variations in catchability, we assumed a uniform distribution of the industrial catch within any month and added this to dhow catches for that month. This obscured the within-month variation in catch. The dhow landings constituted about 53% of the total *P. semisulcatus* landings in the 1994–95 and 1995–96 seasons (Ye et al., 1996); therefore such an assumption would not affect the estimates of monthly catchability significantly. In our study, catchability was assumed to be constant within a month, and the fishing effort data of the *P. semisulcatus* fishery were standardized by using the entire industrial shrimping fleet catch rates, as is customary (Gulland, 1983; Mohammed et al., 1996). The total catch, fishing effort, and abundance index are shown in Table 1.

Table 1

Time series catch, effort, and relative abundance index data of the Kuwait *P. semisulcatus* fishery in the 1994–95 and 1995–96 seasons.

	Catch (10^3number)		Effort (boat-day)		Abundance index	
Time	1994	1995	1994	1995	1994	1995
5 Sep	2007	3752	266.2	357.7		
10 Sep	2212	3165	316.3	325.4		
15 Sep	1565	3201	239.9	352.8	1.000	1.000
20 Sep	1592	4502	260.0	528.8		
25 Sep	1704	1868	295.0	232.5		
30/Sep	1549	1805	282.9	237.1		
5 Oct	1589	1707	490.8	386.0		
10 Oct	782	1342	252.5	316.8		
15 Oct	925	1126	310.9	276.5	0.621	0.613
20 Oct	921	1397	321.1	356.3		
25 Oct	914	1354	329.3	356.9		
30 Oct	724	1051	268.8	285.1		
4 Nov	421	42	199.7	210.6		
9 Nov	396	331	192.0	151.5		
14 Nov	337	411	167.3	191.9	0.500	0.383
19 Nov	287	486	145.4	231.5		
24 Nov	292	404	150.0	195.8		
29 Nov	239	398	124.7	195.7		
4 Dec	460	424	211.5	398.2		
9 Dec	371	369	172.9	350.3		
14 Dec	448	409	210.7	392.1	0.574	0.202
19 Dec	496	311	235.4	301.1		
24 Dec	354	268	169.3	260.6		
29 Dec	703	395	337.8	387.6		
3 Jan	487	383	588.1	378.4		
8 Jan	260	243	315.3	240.9		
13 Jan	347	482	422.3	478.8	0.229	0.201
18 Jan	339	397	413.3	395.0		
23 Jan	339	285	413.6	283.6		
28 Jan	346	272	423.3	271.2		
3 Feb	233	93	529.9	330.2		
8 Feb	45	204	102.3	726.8	0.123	0.057
13 Feb	177	219	402.8	782.2		

Catchability by the UFK fleet is relatively stable within a fishing season. From Equations 1 and 3, $CPUE \cong qN$. CPUE can be an indicator of variation in stock abundance only when catchability q is constant. Figure 1 shows q estimates calculated by simply dividing UFK CPUE data (Siddeek et al., 1989) by the shrimp stock abundance, represented by catch

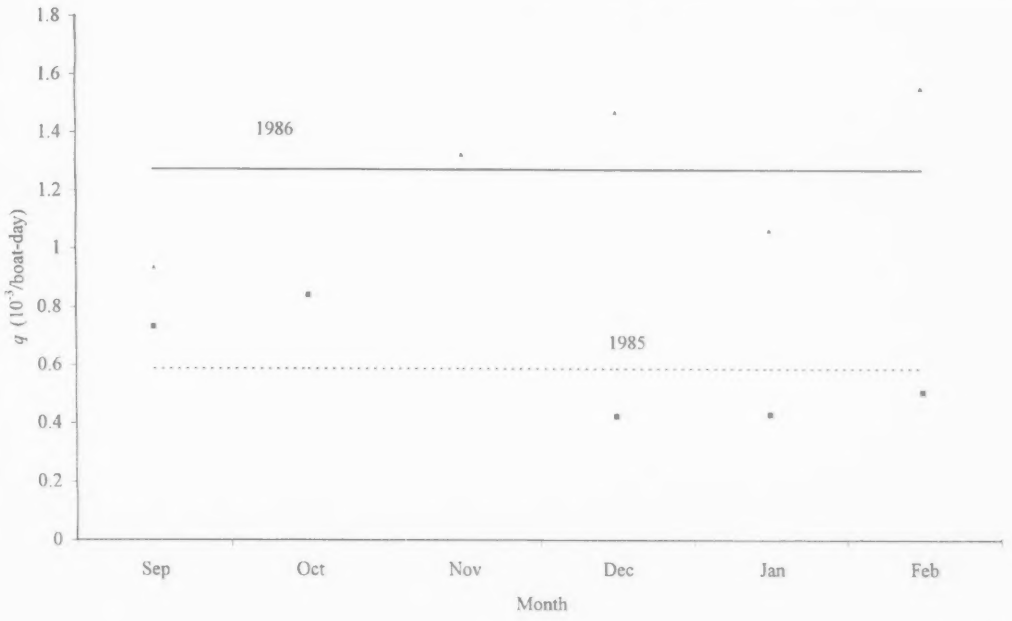


Figure 1

The catchability estimates of the UFK fleet in 1985 (■) and 1986 (▲). The survey catch rates in November 1985 and October 1986 were missing because the whole data set of five year-round surveys was destroyed during the Iraqi occupation in 1991.

rate (kg per haul of 45 minutes) of a survey vessel in 1985 and 1986. There are no survey catch rates in number available, but using catch rate in weight would not introduce any great bias in the investigation of catchability here. The catchability, q, is relatively stable within the period of the investigation, although a great difference can be seen between 1985 and 1986. Therefore, the UFK CPUE was used as an index of stock abundance of *P. semisulcatus* within a fishing season in our study.

Results

Natural mortality is supposed to be known and independent of time within a fishing season, which may violate reality, but this is a more conservative assumption than assuming that natural mortality is constant over periods of years (Hannah, 1995). The natural mortality rate of Kuwait's *P. semisulcatus* has been investigated by a number of authors (Mathews et al., 1987; Siddeek et al., 1989; Xu et al., 1995; Mohammed et al., 1996; FAO[2]; Al-Hossaini[3]); these results range from 1.8 to 4.0/yr. In this study, we used the minimum, median, and maximum estimates of natural mortality rates for our estimation of catchability.

The fits of the above developed depletion model to catch data are shown in Figure 2, in which we used a median natural mortality rate (M=2.9/yr) and produced 95% confidence intervals by the parametric bootstrap (BC) method (Efron and Tibshirani, 1986). The predicted catches for the 1994–95 and 1995–96 seasons are very close to the observed values in general. There is relatively greater discrepancy at the beginning of the seasons, however. The predicted catches are lower than the observed ones in the first month for both seasons (Fig. 2). This is caused by the assumption of Equation 4.

The calculated stock abundance indices also followed the pattern of observed population indices (Fig. 3), showing an exponential depletion of a single co-

[2] FAO (Food and Agriculture Organization of the United Nations). 1982. Assessment of the shrimp stocks of the west coast of the Gulf between Iran and the Arabian Peninsula. Food and Agriculture Organization. FAO Rep. FI:DP/RbyAB/80/015, Rome, Italy, 162 p.

[3] Al-Hossaini, M. 1993. Finfish fisheries and shrimp fisheries management. Tech. Rep., Kuwait Institute for Scientific Research. Food-4 KISR 4367, 53 p.

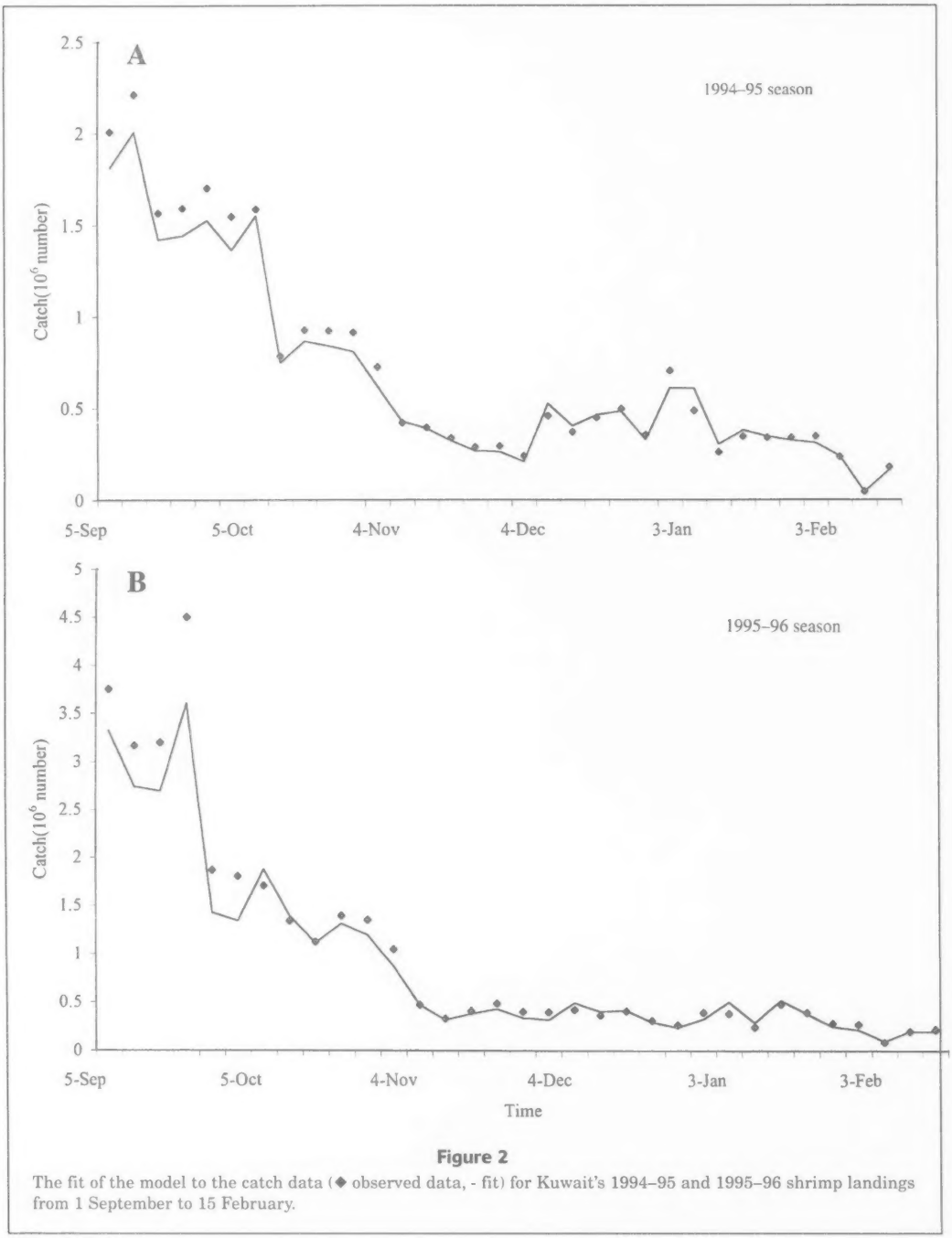


Figure 2

The fit of the model to the catch data (◆ observed data, - fit) for Kuwait's 1994–95 and 1995–96 shrimp landings from 1 September to 15 February.

hort stock. The model fit for the 1995–96 season was better than that for the 1994–95 season. A comparison of these two fits of stock abundance indices showed that the stock experienced a greater decline during the1995–96 season. Figures 2 and 3 demonstrate the goodness of the model fit.

The monthly estimates of catchability in the 1994–95 and 1995–96 seasons exhibit a declining trend as

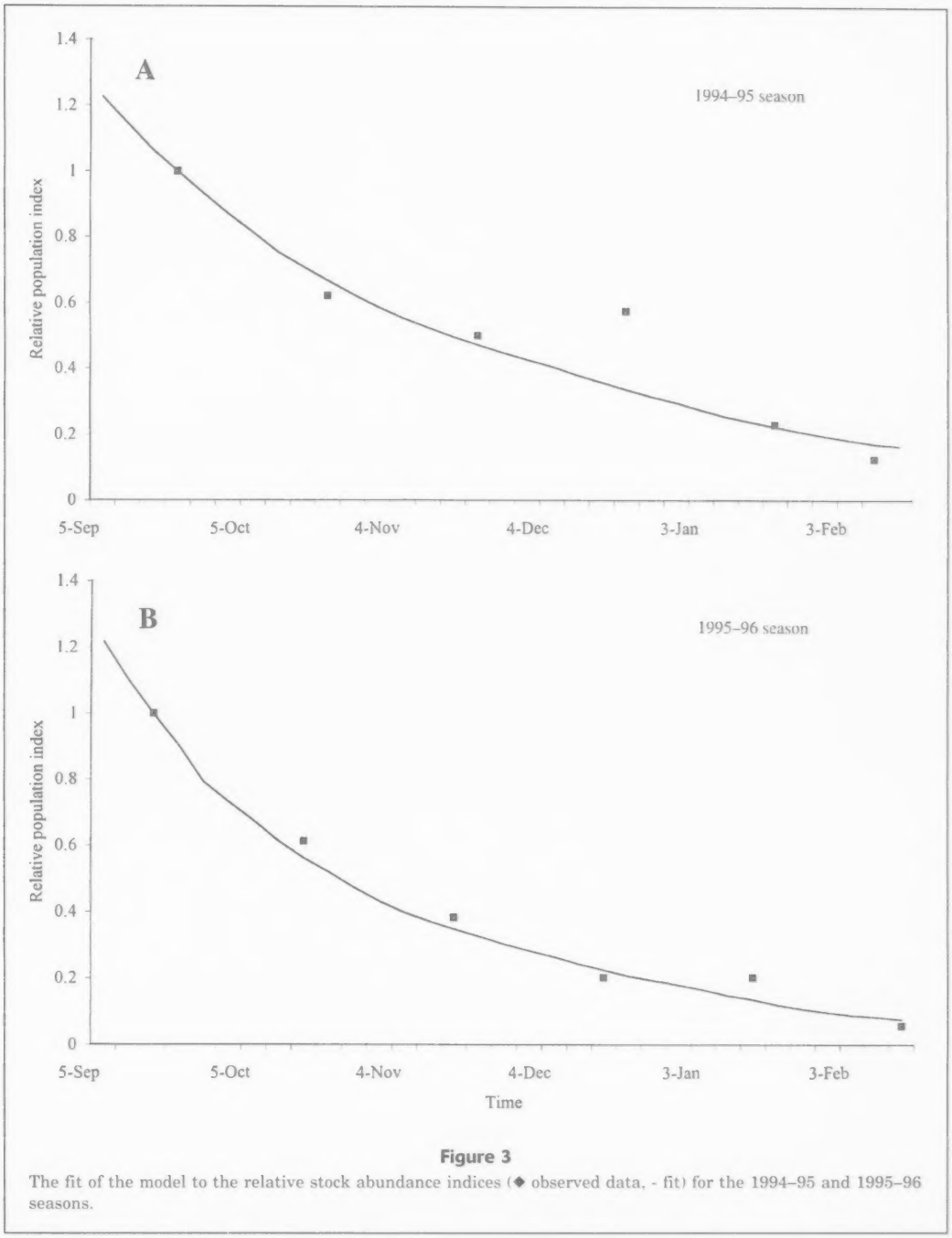


Figure 3

The fit of the model to the relative stock abundance indices (◆ observed data, - fit) for the 1994–95 and 1995–96 seasons.

the season progressed (Fig. 4). From season opening to closing, catchability decreased from 10.40×10^{-5}/boat-day to 4.63×10^{-5}/boat-day in 1994–95, and 17.05×10^{-4}/boat-day to 7.77×10^{-5}/boat-day in 1995–96, respectively (Fig. 4). Comparison between these two seasons shows that shrimp catchability at the beginning of the 1994–95 season was only about 60% of the catchability at the start of the 1995–96 sea-

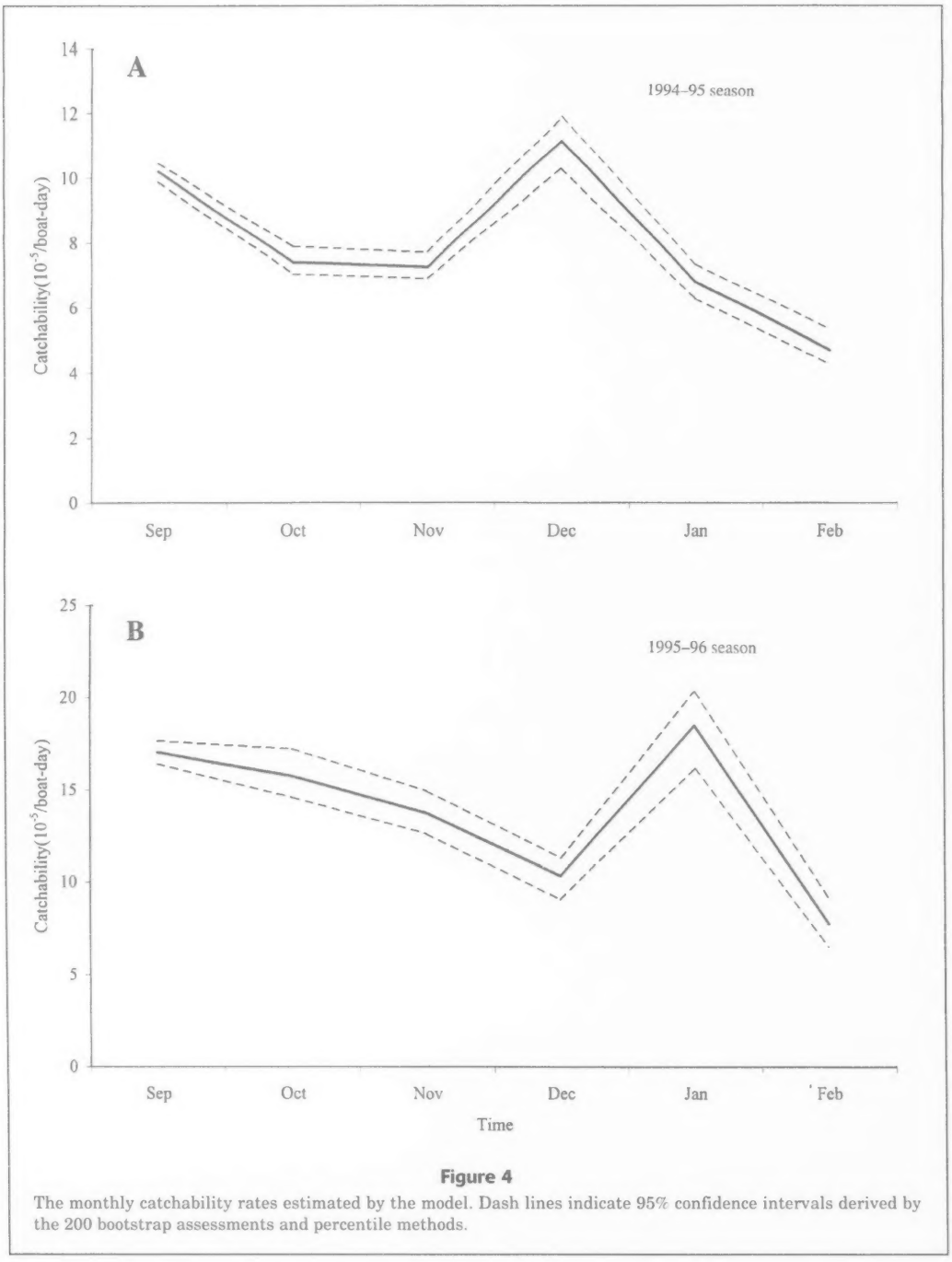


Figure 4

The monthly catchability rates estimated by the model. Dash lines indicate 95% confidence intervals derived by the 200 bootstrap assessments and percentile methods.

son. The estimates of catchability at the end of these two seasons exhibited a similar difference. The catches at the beginning of the 1995–96 season were much higher than those in the same period of the 1994–95 season (Fig. 2). High catchability rates may be associated with abundant stocks. Thus, it can be concluded that high catchability is expected when recruitment is good.

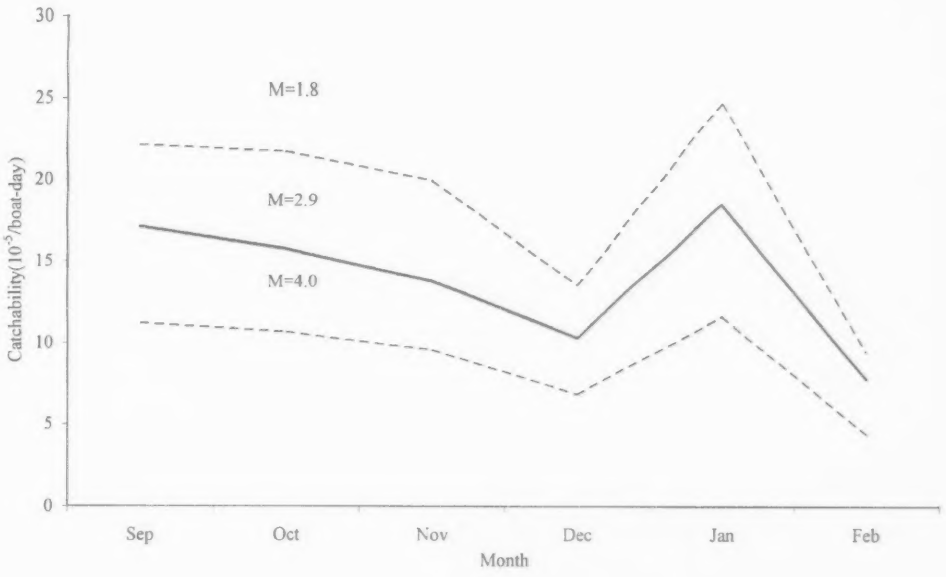


Figure 5
The effect of natural mortality on the estimation of catchability derived from Kuwait's 1995–96 season data.

Another interesting point is that there was a rise in catchability in December for the 1994–95 season, in January for the 1995–96 season. The second catchability rate peak was even slightly higher than the first one in both seasons. All these results show that catchability in the *P. semisulcatus* fishery varies within a fishing season and from year to year, but that the variation patterns in different seasons are similar, with two peaks (Fig. 4).

There are many biases in the estimation of natural morality (Vetter, 1988). The natural mortality rate used in this analysis was the median value of estimates from various sources. Different values of natural mortality will result in different estimates of catchability. Figure 5 shows comparison of the results derived from the seasonal 1995–96 data when the minimum (M=1.8/yr), median (M=2.9/yr), and maximum (M=4.0/yr) estimates of natural mortality were used. The variation of the pattern of catchability was similar within this range of natural mortality. A lower natural morality results in higher catchabilities and a relatively large variation in catchability within a fishing season, demonstrating the correlation between natural mortality and catchability. Therefore, we suggest that the variation pattern derived by this method is reliable, although absolute values may be biased by the natural mortality used.

The weight, W in Equation 5, can be assigned a high or low value depending on the reliability of the auxiliary information compared with the catch data (Hilborn and Walters, 1992). Here, we set W to 6 simply because there were six points of catch and effort data each month, but the auxiliary index had only a single datum point each month. Actually, the auxiliary information was used to constrain the predicted stock's declining track, and thus control total mortality within a certain level. A sensitivity analysis showed that reducing W by 50% resulted in an average decrease of 3.5% in catchability, ranging from 2.1% to 4.8%; increasing W by 50% leads to an increase in catchability of 7.4% on average, with a range of 5.3% to 9.6% (Fig. 6). The primary concern here is the pattern of catchability variation; it is not sensitive to the weighting factor in the case of Kuwait's *P. semisulcatus* fishery (Fig. 6). One method to determine a suitable value for W is by comparing the geometric fits of both the catch and abundance index in the case of unknown reliability over either set of data.

Discussion

An analytical framework to estimate changes in catchability of single cohort fisheries has been pro-

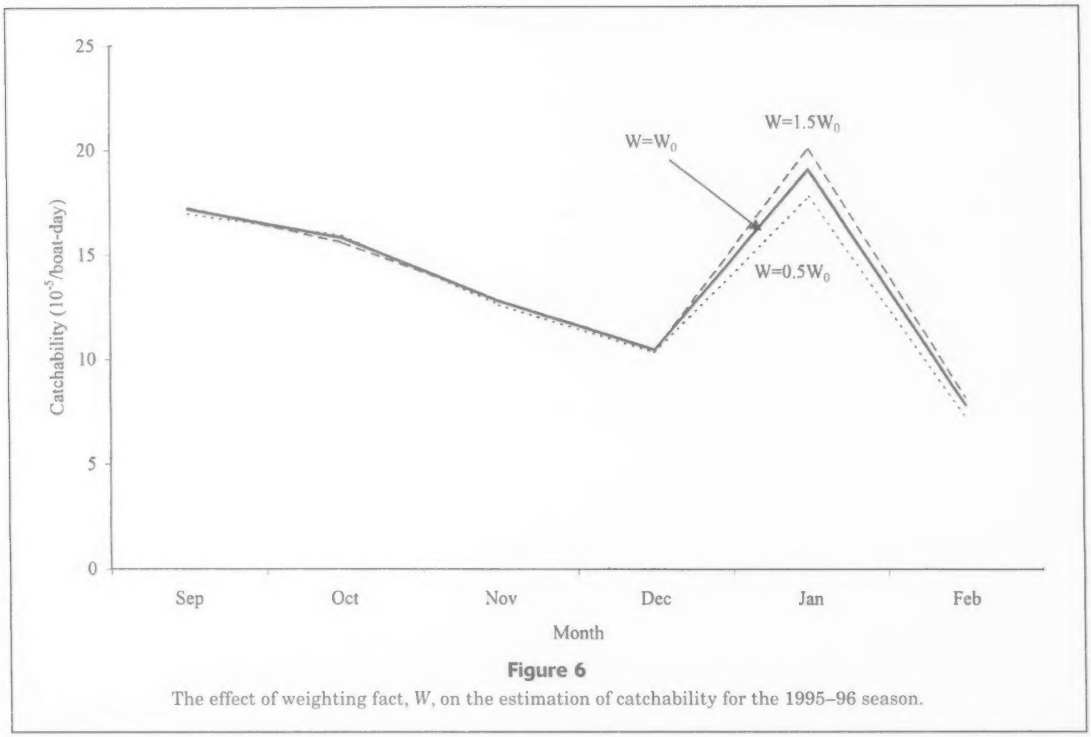


Figure 6

The effect of weighting fact, *W*, on the estimation of catchability for the 1995–96 season.

vided. The results of our study show that the catchability of the Kuwait shrimp fishery is not constant; there were high values at the beginning of the fishing season, lowest values at the end. The two-peak pattern of catchability may be associated with schooling behavior at the time of recruitment to the fishery and the spawning migration of the species. There is also great variation in catchability on an interannual basis because schooling is associated with high recruitment (Mathews et al., 1994) and certain environmental conditions (Penn, 1984).

The general declining trend in catchability may be attributed to schooling behavior. As fishing progressed, shrimp schools were depleted or dispersed, and catchability declined (Drobisheva and Aseev, 1976; Garcia and Reste, 1981; van Zalinge, 1984; Mathews et al., 1994). Reduced activity caused by low temperature is another identified cause for the decline of catchability of Spencer Gulf prawns (*Penaeus latisulcatus*) in Australia during the winter months (June to August) (Sluczanowski, 1984) and *P. semisulcatus* in Kuwait (Mathews and Al-Hossaini, 1982). Both schooling and effects of decreasing temperature likely contributed to the variation of catchability in the Kuwait shrimp fishery.

The major spawning season for *P. semisulcatus* is from December to April (Drobisheva and Aseev, 1976; Siddeek et al., 1989). Many penaeids undertake a short shoreward migration before spawning (Garcia, 1988; Ye, 1984). *Penaeus semisulcatus* in the Gulf of Carpentaria migrate from offshore into shallow waters in the spring before spawning (Dall et al., 1990). Drobisheva and Aseev (1976) reported that *P. semisulcatus* in the Arabian Gulf forms prespawning schools or aggregations in the spawning area. Although the migration pattern of *P. semisulcatus* in watters off Kuwait is still not clear, the pattern of catchability strongly indicates that this species may return to Kuwait waters before spawning season and concentrate in certain areas. Such shoreward movement by spawning schools resulted in the highest catchability, and a peak in December or January (Fig. 4), which rapidly decreased as fishing progressed.

There is also the possibility that shrimp of non-Kuwait origin migrate to Kuwait waters. El-Musa (1982) analyzed mark-recapture data and concluded that the *P. semisulcatus* released in February 1979 at Dohat Al-Zaur, close to the border with Saudi Arabia, exhibited a strong northward movement. The timing of such a migration could be affected significantly by environmental conditions associated with a spawning migration, resulting in an apparent increase in catchability earlier in some years than in others.

The schooling behavior of *P. semisulcatus* was associated with years of higher catches (van Zalinge, 1984; Mathews et al., 1994). When recruitment to the fishery was good, larger schools, and thus higher catchability, could be expected. The catches at the beginning of the 1995–96 season were much higher than those of the same period in the 1994–95 season (Fig. 2); catchability in 1995–96 was also much higher (Fig. 4). With intensive fishing effort, the shrimp stock was reduced to a very low level by the end of the fishing season, despite its initial abundance. Therefore, catchability is associated with stock abundance.

Although the variation in total mortality and catch cannot be explained by variation in natural mortality, violation of the assumption that natural mortality remains constant within a season may still be the source for biases in the estimation of monthly catchability. The relatively larger discrepancy between predicted and observed catches, the predicted being always lower than the observed, in the first month (Fig. 2) may result from a departure from the natural mortality rate that is generally used. An inflated natural mortality for the first month will give lower predicted catches because the first month's catchability was related to the initial population number, which in turn was connected to all the other estimates of catchability in the fitting scheme used in this study. The fit cannot be improved by adjusting catchability for the first month. Although it may be true that natural mortality is constant during a fishing season, a possible second recruitment in early September, which was not considered in our study and is probably rather weak, may compensate natural death to some extent and lead to a lower net natural mortality than the value we used.

This study reports apparent changes in catchability of Kuwait's *P. semisulcatus* fishery. It should be noted that M, q, CPUE, and schooling must be interrelated to a certain extent. Schooling may bias CPUE with respect to years in which it does not occur, and M estimates from any method applied in Kuwait may also be influenced if schooling occurs only in certain seasons. Changes in catchability to a fishery may be associated with both fishing power and population characteristics. A better understanding of the mechanisms underlying these results will improve stock assessment. The variations in catchability suggest that changes in catch-rate indices may not actually reflect variations in abundance. Although other results support the conclusion of this study, functional relationships among catchability and population characteristics, fleet characteristics, and environmental conditions should be studied further.

Acknowledgments

This study was part of the Shrimp Fisheries Management Project supported by the Kuwait Institute for Scientific Research. We would like to thank James Bishop for many constructive discussions and comments on the manuscript, and two anonymous referees for extensive reviews. The contributions of the project staff are highly appreciated.

Literature cited

Abdul-Ghaffar, A. R., and A. Y. Y. Al-Ghunaim.
1994. Review of the Kuwait's shrimp fishery, their development and present status. Proceedings of the technical consultation on shrimp management in the Arabian Gulf, Al Khobar, 6–8 November 1994, Saudi Arabia, p 1–26.

Arreguin-Sanchez, F.
1996. Catchability: a key parameter for fish stock assessment. Rev. Fish Biology Fisheries 6:221–242.

Atran, S. M., and J. G. Loesch.
1995. An analysis of weekly fluctuations in catchability coefficients. Fish. Bull. 93(3):562–567.

Chittelborough, R. G.
1970. Studies on recruitment of the western Australian rock lobster *Panulirus longipes cygnus* George: density and natural mortality of juveniles. Aust. J. Mar. Freshwater Res. 21:131–48.

Csirke, J.
1989. Changes in the catchability coefficient in the Peruvian anchoveta (*Engraulis ringens*) fishery. *In* D. Pauly, P. Muck, J. Mendo, and I. Tsukayama (eds.),The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conf. Proceedings 18, Manila, Philippines, p 207–219.

Dall, W., B. J. Hill, P. C. Rothlisberg, and D. J. Staples.
1990. The biology of the Penaeidae. Adv. Mar. Biol. 27: 1–489.

Drobisheva, S. S., and Y. P. Aseev.
1976. On the life cycle of *Penaeus semisulcatus* /Crustacea, Decapoda, Penaeidae/ in the Persian Gulf. Zoologicheskij Zhurnal 5/s/:769–771.

Efron, B., and R. Tibshirani.
1986. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. Statistical Sci. 1(1):54–77.

El-Musa, M.
1982. Migration patterns and growth rates for *Penaeus semisulcatus* using mark recapture experiments in Kuwait. *In* C. P. Mathews (ed.), Revised proceedings of the shrimp fisheries management workshop. Kuwait Institute for Scientific Research, Kuwait, p. 172–206.

Garcia, S.
1988. Tropical penaeus prawns. *In* J. A. Gulland (ed.), Fish population dynamics, 2nd ed. John Wiley, Chichester, p 219–249.

Garcia, S., and L. Le Reste.
1981. Life cycles, dynamics, exploitation and management of coastal penaeid shrimp stocks. FAO Fish. Tech. Pap. 203, FAO, Rome, 215 p.

Gulland, J. A.
1983. Fish stock assessment: a manual of basic methods. Wiley, New York, NY, 233 p.

1989. The optimum opening date in shrimp fishing; a sensitivity analysis. *In* Proceedings of the eighth shrimp and fin fisheries management workshop. Kuwait Bull. Mar. Sci. 10:71–79.

Hannah, R. W.
1995. Variation in geographic stock area, catchability, and natural mortality of ocean shrimp (*Pandalus jordani*): some new evidence for a trophic interaction with Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 52:1018–1029.

Hilborn, R., and C. J. Walters.
1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York, NY, 570 p.

Hill, B. J.
1985. Effect of temperature on duration of emergence, speed of movement, and catchability of the prawn *Penaeus esculentus*. *In* P. C. Rothlisberg, B. J. Hill, and D. J. Staples (eds.), Proceedings of the second Australian national prawn seminar. Simpson Halligan, Brisbane, Australia, p. 77–83.

MacCall, A. D.
1976. Density dependence of catchability coefficient in the California Pacific sardine, *Sardinops sagax caerulea*, purse seine fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 18:136–148.
1990. Dynamic geography of marine fish populations. Washington Sea Grant Program, Seattle, WA, 153 p.

Mathews, C. P.
1994. Fisheries management: the Kuwaiti experience. Mar. Fish. Rev. 56(1):23–30.

Mathews, C. P. and M. Al-Hossaini.
1982. Stock assessment of Kuwait's shrimp populations, growth, mortality and life cycles *of Penaeus semisulcatus, Metapenaeus affinis* and *Parapenaeopsis stylifera*, and management of Kuwait's shrimp stocks. Proceedings of the third shrimp and fin fisheries management workshop, fin fisheries session, 4–5 December, 1982, p. 112–172.

Mathews, C. P., M. Al-Hossaini, A. R. Abdul Ghaffar, and M. Al-Shoushani.
1987. Assessment of short-lived stocks with special reference to Kuwait's shrimp fisheries: a contrast of results obtained from traditional and recent size-based techniques. *In* D. Pauly and G. R. Morgan (eds.), Length-based methods in fisheries research, p. 147–166. ICLARM Conf. Proc. 13.

Mathews, C. P., S. Kedidi, J. Al-Qader, I. Al-Qader, A. H. Radhi, N. I. Fita, and A. Al-Yahya.
1994. *Peneaus semisulcatus* stocks of the western Gulf: effects of schooling and environmental variation on interstock modelling and management of Kuwaiti, Saudi Arabian and Bahraini stocks. Proceedings of the technical consultation on shrimp management in the Arabian Gulf, 6–8 November 1994, Al Khobar, Saudi Arabia, p. 1–47.

Mathews, C. P., and M. Samuel.
1991. Management and research strategies in Kuwait's trawl fishery. ICES Sci. Symp. 193:330–340.

Mohammed, H. M. A., J. M. Bishop, and X. Xu.
1996. Population characteristics of green tiger prawn, *Penaeus semisulcatus*, in Kuwait waters prior to the Gulf War. Hydrobiologia 337:37–47.

Morgan, G. R.
1974. Aspects of the population dynamics of the western rock lobster *Panulirus cygnus* George. II. Seasonal changes in the catchability coefficient. Aust. J. Mar. Freshwater Res. 25:249–59.
1989. Separating environmental and fisheries effects in the recruitment of Gulf shrimp. Kuwait Bull. Mar. Sci. 10: 51–59.

Murphy, G.
1977. Characteristics of clupeoids. *In* J. A. Gulland (ed.), Fish population dynamics, 1st ed. John Wiley and Sons, New York, NY, p. 283–308.

Penn, J. W.
1984. The behaviour and catchability of some commercially exploited penaeids and their relationship to stock and recruitment. *In* J. A. Gulland and B. J. Rothschild (eds.), Penaeid shrimps: their biology and management. Fishing News Books, Farnham, Surrey, p. 173–186.

Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

Siddeek, M. S. M., and A. R. Abdul-Ghaffar.
1989. The effects of the one month delay in opening the shrimp fishing season of *Penaeus semisulcatus* in 1986 in Kuwait waters. Kuwait Bull. Mar. Sci.10:81–96.

Siddeek, M. S., J. M. Bishop, M. El-Musa, A. R. Abdul-Ghaffar, and M. S. Abdulla.
1994. Possible reasons for increased landings of Kuwait's green tiger shrimp (*Penaeus semisulcatus*) in the late 1980s. *In* L. M. Chou et al. (eds.) Proceedings of the third Asian fisheries forum, Manila, Philippines, p. 224–227.

Siddeek, M. S. M., M. El-Musa, and A. R. Abdul-Ghaffar.
1989. Final report of the shrimp fisheries management project Phase V (MB-70). Kuwait Institute for Scientific Research, Kuwait, Pre. No. KISR 3156, 104 p.

Sluczanowski, P. R.
1984. Modelling and optimal control: a case study based on the Spencer Gulf prawn fishery for *Penaeus latisulcatus* Kishinouye. J. Cons. Int. Explor. Mer 41:211–225.

van Zalinge, N. P.
1984. The shrimp fisheries in the Gulf between Iran and the Arabian Peninsula. *In* J. A. Gulland and B. J. Rothschild (eds.), Penaeid shrimps: their biology and management. Fishing News Books, Farnham, England, p 71–83.

Vetter, E. F.
1988. Estimation of natural mortality in fish stocks: a review. Fish. Bull. 86(1):25–43.

Wassenberg, T. J., and B. J. Hill.
1990. Moulting behaviour of the tiger prawn *Penaeus esculentus* (Haswell). Aust. J. Mar. Freshwater Res. 35:561–71.

Winters, G. H., and J. P. Wheeler.
1985. Interaction between stock area, stock abundance, and catchability coefficient. Can. J. Fish. Aquat. Sci. 42:989–998.

Xu, X., J. M. Bishop, H. M. A. Mohammed, and A. H. Alsaffar.
1995. Estimation of the natural mortality rate of green tiger prawns *Penaeus semisulcatus* (De Hann, 1884) in Kuwait waters using relative abundance data. J. Shellfish Res. 14(1):179–184.

Ye, C. C.
1984. The prawn (*Penaeus orientalis* Kishinouye) in Pohai Sea and their fishery. *In* J. A. Gulland and B. J. Rothschild (eds.), Penaeid shrimps: their biology and management. Fishing News Books, Farnham, England, p 49–59.

Ye, Y., H. M. A. Mohammed, and J. M. Bishop.
1996. An overview of the shrimp resources and fisheries in Kuwait waters. Tech. Rep. Kuwait Institute for Scientific Research, 33 p.

Straying of adult sockeye salmon, *Oncorhynchus nerka*, entering a non-natal hatchery

Jason N. Griffith

Andrew P. Hendry

Thomas P. Quinn

School of Fisheries
University of Washington
Box 357980, Seattle, Washington 98195
E-mail address (for T. P. Quinn, contact author): tquinn@fish.washington.edu)

Salmonid fishes tend to return to their natal site ("home") for reproduction (topic reviewed by Quinn and Dittman, 1992; Quinn, 1993). Odors learned by juveniles during freshwater residence and downstream migration guide adults during the final stages of homing migration (Hasler and Scholz, 1983; Dittman and Quinn, 1996), although adults also respond to spawning site characteristics (Blair and Quinn, 1991) and odors of conspecifics (Newcombe and Hartman, 1973; Honda, 1982; Groot et al., 1986). However, some salmonids do not return to their natal site, but instead "stray" and spawn elsewhere (Quinn, 1993).

The terms "homing" and "straying" are defined by the endpoints of migration (i.e. the natal or non-natal site, respectively), but during their migration some salmonids ascend one stream, only to later leave and spawn elsewhere (Ricker and Robertson, 1935; Ricker, 1972). Mature salmonids respond to the stimulus of imprinted odors with positive rheotaxis and move downstream when they no longer detect home odors (Johnsen and Hasler, 1980); therefore movement up a non-natal stream does not necessarily mean that the fish will spawn there. It may be natural for salmon migrating up complex river systems to ascend non-natal streams for a brief distance before the absence of homestream odors triggers negative rheotaxis. However, the behavior of some fish is not adequately explained by such "proving" behavior. For example, 16% of the sockeye salmon (*Oncorhynchus nerka*) radio-tagged by Burger et al. (1995) in Tustumena Lake that eventually spawned in a particular tributary, initially entered a different tributary and stayed there for up to one week. In addition, 21% of the fish that spawned on the shoreline of the lake had previously entered a tributary stream. These fish might be "exploring" (actively seeking different sites and comparing their attributes) or "wandering" (searching in the absence of stimuli).

Unfortunately, the principal methods for studying homing fail to distinguish straying from exploring or other related behavior patterns. One approach is to collect adult salmon from spawning grounds, displace them to another spawning site or to a nonspawning area, and monitor their subsequent movements. Most of the fish returned to the site of their capture (e.g. Hartman and Raleigh, 1964; McCart, 1970; Varnavskiy and Varnavskiy, 1985; Blair and Quinn, 1991), and the authors assumed but did not verify that the capture site was home. Another approach is to capture and track adults as they move upstream to their spawning site (e.g. Berman and Quinn, 1991; Burger et al., 1995). In these studies, the final spawning location is assumed to be the natal one but this also is not verified.

The primary alternative approach to capturing and marking adult salmon is to mark them as juveniles and monitor the locations where they subsequently spawn (e.g. Quinn and Fresh, 1984; Quinn et al., 1991; Pascual and Quinn, 1994; Vander Haegen and Doty, 1995). The origin of these salmon is known, but once they enter a hatchery, they cannot leave and are only identified as strays after they are killed. Much of what we know about the frequency of straying is based on data from hatchery populations, but these data reveal little about the processes of homing and straying and may not represent wild populations (Quinn, 1993). Information on the extent to which salmon that enter a non-natal hatchery would leave, if given the opportunity, would provide insights into migratory behavior and the potential biases of estimating the extent of straying from hatchery populations.

The University of Washington hatchery (UWH) provides an excellent opportunity to study homing, exploring, and straying of salmon. The UWH releases chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon smolts each spring. Sockeye salmon are abundant elsewhere in the Lake Washington watershed, and a few enter the UWH although they are not reared there. In our study, all adult sockeye that entered the UWH were tagged and released just outside the hatchery. If they were proving or exploring, we would not expect them to re-enter the UWH. However, if they returned repeatedly after release, it would indicate that they would

Manuscript accepted 15 September 1998.
Fish. Bull. 97:713–716 (1999).

probably spawn at this non-natal site. We also tagged and released chinook salmon to compare the behavior of salmon that originated elsewhere (the sockeye) with that of salmon that presumably originated from the hatchery (the chinook).

Methods

The UWH is located approximately 10 km from Puget Sound, Washington, on the north side of Portage Bay, in the Lake Washington system (Fig. 1). It produces chinook and coho but not sockeye salmon. However, an average of eight sockeye salmon (range 4–18) entered the pond each fall during the years of this study (1992–97). Over this period, the Lake Washington system has had a mean total sockeye escapement of 175,893 (range 122,415–400,000).[1] The main spawning areas within the watershed are the Cedar River, Issaquah Creek, and Bear Creek, and all sockeye salmon spawn in the watershed upstream from the UWH outfall (Fig. 1; Hendry et al., 1996), principally in October and November.

During the years of our study, an average of 1299 chinook salmon (range 458–2229) entered the UWH, principally from early October through mid-November. Analysis of coded wire tagging (CWT) data has revealed a very high fidelity of UW salmon for the hatchery, and very low levels of straying of non-natal chinook salmon into the UWH (>>99% of the fish entering the hatchery had been released from it; Quinn and Dittman, 1992). We therefore assumed that chinook salmon entering the hatchery had been produced there but a few might have been produced elsewhere.

Twice each week during the fall, the UWH pond was partially drained and all the salmon were seined into a small area. All sockeye salmon and a subsample of the chinook salmon (in 1994–96) were transferred from the seine to a live box in the pond. These fish were tagged with a T-bar tag on each side in the musculature just below the dorsal fin and quickly released within 10 m of the ladder leading into the hatchery. All tagged chinook salmon were males (1 year olds in 1994; 2 year olds in 1995 and 1996) and releases were spread throughout the course of the run. Returning tagged fish of both species were recaptured during the seining of the pond. Those in good condition were released once more outside the hatchery but those with extensive fungus on their bodies were sacrificed. Fish that returned a third time were killed, regardless of their condition.

[1] Egan, R. 1998. Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, WA 98501. Personal commun.

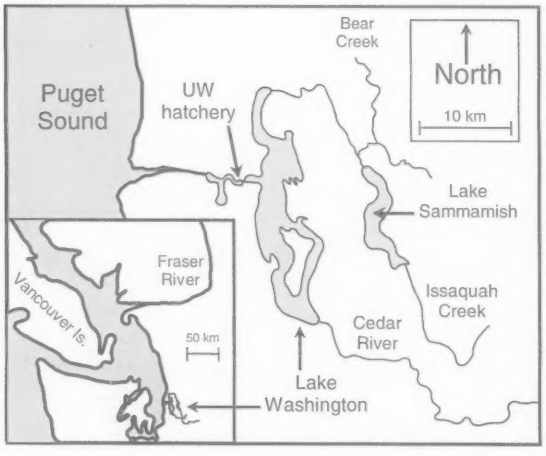


Figure 1

Map of the Lake Washington drainage, showing locations of the University of Washington (UW) hatchery and the major tributaries used by spawning sockeye salmon. Insert indicates the drainage's location in northwest Washington.

Results

Between 1992 and 1997, 48 sockeye salmon (28 males and 20 females) entered the UW hatchery and were tagged and released (Table 1). The percentage of these fish that returned to the hatchery varied from 0% to 37.5% among years with an overall mean of 20.8% (Table 1). Of the ten sockeye salmon that returned after their first displacement and that were displaced a second time, five (50%) returned again. The sex ratio of the sockeye salmon straying into the hatchery (58% males) was similar to that of those returning after displacement (60% males).

From 1994 to 1996, 132 male chinook salmon were tagged and released from the UWH (Table 1). The proportion of chinook salmon that returned after displacement did not differ among the three years (χ^2=0.015, 2 df, P>0.99, overall mean=77%, Table 1). The percentage of sockeye salmon returning after displacement was much smaller than that of the chinook salmon (20.8% vs. 77.3%; χ^2=48.5, 1 df, P<0.005). Of the chinook salmon that returned after release, 65% returned a second time.

Discussion

Our finding that most of the sockeye entering the UWH appeared to be proving or exploring rather than

Table 1

Number of adult sockeye and chinook salmon tagged and released from the University of Washington hatchery (1992–97) and numbers returning to the hatchery once and twice. Numbers in parentheses represent percentages of returning fish: percentages of those returning once are based on the total number released; percentages of those returning twice are based on the number returning once.

Species	Year	Number tagged	Numbers of fish returning	
			Once	Twice
Sockeye	1992	4	0 (0)	0 (0)
	1993	6	1 (16.7)	0 (0)
	1994	8	1 (12.5)	0 (0)
	1995	4	1 (25.0)	1 (100)
	1996	18	4 (22.2)	4 (100)
	1997	8	3 (37.5)	0 (0)
	Total	48	10 (20.8)	5 (50.0)
Chinook	1994	32	25 (78.1)	13 (52.0)
	1995	39	30 (76.9)	17 (56.7)
	1996	61	47 (77.0)	36 (76.5)
	Total	132	102 (77.2)	66 (64.7)

straying in the true sense is helpful in interpreting the movements of salmon during the final stages of their homing migration. Most of the sockeye (38 of 48) that entered the UWH and were released did not return again. From our data we cannot determine which term (proving, exploring, or wandering) best describes their behavior. However, five out of ten of the sockeye that returned once returned a second time after displacement. We do not understand the motivation for the behavior of these fish but interpret their persistence as evidence that they would have spawned at the site and thus were considered strays in the true sense.

Why did only 10 of 48 sockeye salmon re-enter the UWH? Were the others unable to locate the hatchery or did they die prior to re-entry? The proportion of chinook salmon returning to the UWH after displacement (77%) was much higher than that of sockeye salmon, suggesting that the UWH was not difficult to find and re-enter after displacement. The proportion of chinook salmon returning in this study was similar to or higher than those reported in previous studies that displaced chinook about 5 km from the UWH (Whitman et al., 1982; Brannon et al., 1986, Quinn et al., 1988). A few of the tagged sockeye in the present study returned over two weeks after release, implying that the sockeye had sufficient time to find and re-enter the UWH before they were too weak.

The 48 sockeye salmon that initially entered the UWH were only 0.005% of the total run of sockeye salmon to the Lake Washington system during the years of this study. We do not infer that this extremely low rate of straying or exploring is representative of spawning sites within this or other lake systems. The absence of odors from conspecific juveniles and trace odors from adults emanating from the UWH might make it less attractive than rivers perennially used by sockeye (Groot et al., 1986), and the small discharge and lack of appropriate habitat for spawning might also deter non-native sockeye from entering. Likewise, the proportions of sockeye salmon straying and exploring in our study may not be representative of those for natural systems.

Entry of sockeye salmon into UWH may differ in some respects from their behavior in natural systems but exploring and straying are characteristic of salmon. On the basis of our results, many of the salmon that enter non-natal hatcheries and that are classified as strays might have left if given the chance. Studies of straying based on recoveries in hatcheries may thus overestimate straying rates, at least in some cases (Quinn et al. 1991). The lack of quantified estimates of proving or exploring behavior makes it difficult to assess whether the high proportion of these patterns found in our study is typical of sockeye or Pacific salmon in general. The distinction between straying and exploring is important to the management of Pacific salmon because CWT-based straying estimates from hatchery populations are commonly used to model interactions between hatchery and wild populations (Grant, 1997), and this subject needs further research.

Acknowledgments

We thank William Hershberger, Glenn Yokoyama, Heather Roffey, Jainrong Chang, and undergraduate students for assisting with salmon collection and tagging, and Andrew Dittman, Jeffrey Silverstein, Fred Utter, and Carl Burger for comments on the manuscript. Floy Tag Co. donated tags and a tagging gun. Andrew Hendry was supported by the H. Mason Keeler Endowment and a Natural Sciences and Engineering Research Council of Canada postgraduate scholarship.

Literature cited

Berman, C. H., and T. P. Quinn.
1991. Behavioural thermoregulation and homing by spring chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. J. Fish Biol. 39:301–312.

Blair, G. R., and T. P. Quinn.
1991. Homing and spawning site selection by sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. Can. J. Zool. 69:176–181.

Brannon, E. L., T. P. Quinn, R. P. Whitman, A. E. Nevissi, R. E. Nakatani, and C. D. McAuliffe.
1986. Homing of adult chinook salmon after brief exposure to whole and dispersed crude oil. Trans. Am. Fish. Soc. 115:823–827.

Burger, C. V., J. E. Finn, and L. Holland-Bartels.
1995. Patterns of shoreline spawning by sockeye salmon in a glacially turbid lake: evidence for subpopulation differentiation. Trans. Am. Fish. Soc. 124:1–15.

Dittman, A. H., and T. P. Quinn.
1996. Homing in Pacific salmon: mechanisms and ecological basis. J. Exp. Biol. 199:83–91.

Grant, W. S. (editor).
1997. Genetic effects of straying of non-native hatchery fish into natural populations: proceedings of the workshop June 1–2, 1995, Seattle, Washington. U.S. Dep. Commer., NOAA, NMFS Tech. Memo. NMFS-NWFSC-30, 122 p.

Groot, C., T. P. Quinn, and T. J. Hara.
1986. Responses of migrating adult sockeye salmon (*Oncorhynchus nerka*) to population specific odors. Can. J. Zool. 64:926–932.

Hartman, W. L., and R. F. Raleigh.
1964. Tributary homing of sockeye salmon at Brooks and Karluk lakes, Alaska. J. Fish. Res. Board Can. 21:485–504.

Hasler, A. D., and A. T. Scholz.
1983. Olfactory imprinting and homing in salmon. Springer-Verlag, Berlin, 134 p.

Hendry, A. P., T. P. Quinn, and F. M. Utter.
1996. Genetic evidence for the persistence and divergence of native and introduced sockeye salmon (*Oncorhynchus nerka*) within Lake Washington, Washington. Can. J. Fish. Aquat. Sci. 53:823–832.

Honda, H.
1982. On the female pheromones and courtship behaviour in the salmonids, *Oncorhynchus masou* and *O. rhodurus*. Bull. Jpn. Soc. Sci. Fish. 48(1):47–49.

Johnsen, P. B., and A. D. Hasler.
1980. The use of chemical cues in the upstream migration of coho salmon, *Oncorhynchus kisutch* Walbaum. J. Fish Biol.17:67–73.

McCart, P. J.
1970. A polymorphic population of *Oncorhynchus nerka* at Babine Lake, B.C. involving anadromous (sockeye) and non-anadromous (kokanee) forms. Ph. D. diss., Univ. British Columbia, Vancouver, 135 p.

Newcombe, C., and G. Hartman.
1973. Some chemical signals in the spawning behavior of rainbow trout *(Salmo gairdneri)*. J. Fish. Res. Board Can. 30:995–997.

Pascual, M. A., and T. P. Quinn.
1994. Geographical patterns of straying in fall chinook, *Oncorhynchus tshawytscha* (Walbaum), from Columbia River (USA) hatcheries. Aquacult. Fish. Manage. 25 (suppl. 2):17–30.

Quinn, T. P.
1993. A review of homing and straying of wild and hatchery-produced salmon. Fish. Res. 18:29–44.

Quinn, T. P., and A. H. Dittman.
1992. Fishes. *In* F. Papi (ed.), Animal homing, p. 145–211. Chapman and Hall, London.

Quinn, T. P., and K. Fresh.
1984. Homing and straying in chinook salmon (*Oncorhynchus tshawytscha*) from Cowlitz River Hatchery, Washington. Can. J. Fish. Aquat. Sci. 41:1078–1082.

Quinn, T. P., A. F. Olson, and J. T. Konecki.
1988. Effects of anaesthesia on the chemosensory behaviour of Pacific salmon. J. Fish Biol. 33:637–641.

Quinn, T. P., R. S. Nemeth, and D. O. McIsaac.
1991. Homing and straying patterns of fall chinook salmon in the lower Columbia River. Trans. Am. Fish. Soc. 120:150–156.

Ricker, W. E.
1972. Hereditary and environmental factors affecting certain salmonid populations. *In* R. C. Simon and P. A. Larkin (eds.), The stock concept in Pacific salmon, p. 19–160. H. R. MacMillian Lectures in Fisheries, Univ. British Columbia, Vancouver, B.C.

Ricker, W. E., and A. Robertson.
1935. Observations on the behavior of adult sockeye salmon during the spawning migration. Can. Field-Nat. 49:132–134.

Vander Haegen, G. and D. Doty.
1995. Homing of coho and fall chinook salmon in Washington. Wash. Dep. Fish Wildlife Tech. Rep. H95-08:68 p.

Varnavskiy, V. S., and N. V. Varnavskiy.
1985. Assessment of straying between groups of early spawning sockeye salmon, *Oncorhynchus nerka*, in Nakhichinskoye Lake, Kamchatka. J. Ichthyol. 25:136–139.

Whitman, R. P., T. P. Quinn, and E. L. Brannon.
1982. Influence of suspended volcanic ash on homing behavior of adult chinook salmon. Trans. Am. Fish. Soc. 111:63–69.

Oceanic feeding habits of chinook salmon, *Oncorhynchus tshawytscha*, off northern California

Sharon L. Hunt

Timothy J. Mulligan

Department of Fisheries
Humboldt State University, Arcata, California 95521
E-mail address (for T. J. Mulligan, contact author): tjm2@axe.humboldt.edu

Kenichiro Komori

School of Biological Sciences
Macquarie University, New South Wales 2109, Australia

The chinook salmon, *Oncorhynchus tshawytscha*, is an important commercial and recreational species inhabiting rivers and nearshore coastal waters from San Diego, California, to the Bering Sea and Japan (Miller and Lea, 1972). Many West Coast populations are in a serious decline (Pearcy, 1992). Nehlsen et al. (1991) reported an overall decrease in salmonid numbers in the coastal waters of the Pacific Northwest and suggested that northern California chinook salmon runs may be at high risk of extinction owing to 1) habitat damage and mainstream passage problems; 2) overharvesting; and 3) hybridization, predation, competition, disease, and poor ocean survival conditions. Surprisingly, little research has been done off the northern California coast regarding the diet of salmonids during oceanic migrations.

Studies on the feeding habits of adult chinook salmon have been conducted from San Francisco, California, to southeastern Alaska. Northern anchovy (*Engraulis mordax*), juvenile rockfishes (*Sebastes* spp.), euphausiids, Pacific herring (*Clupea pallasii*), osmerids, and crab megalopae (*Cancer magister*) have been reported as main prey items of chinook salmon ranging from San Francisco to the Washington coast (Heg and Van Hyning, 1951; Merkel, 1957; Petrovich, 1970; Brodeur et al., 1987). Various studies conducted in more northern regions of the Eastern Pacific Ocean have shown Pacific herring and Pacific sandlance (*Ammodytes hexapterus*) as dominant food items (Pritchard and Tester, 1944; Reid, 1961; Prakash, 1962). All of the above studies noted seasonal and or annual differences in the dominant prey items. Overall, it appears that northern anchovy and rockfishes are the most important prey items for chinook salmon in southern coastal regions (i.e. San Francisco Bay area) whereas the importance of Pacific herring and Pacific sandlance increases in more northern regions (Healey, 1991). To adequately describe the trophic resources utilized by a fish population, it is necessary to sample at consistent times throughout the year (Bowen, 1996). Furthermore, in an upwelling zone, such as northern California, the food habits of many fish species may fluctuate considerably between years owing to environmental variability (Brodeur and Pearcy, 1992). For example, diets of pelagic nekton may vary owing to changes in oceanographic conditions, such as onshore and alongshore transport, primary productivity, and prey abundances (Brodeur et al., 1987). In our study, we examined the diet of chinook salmon off northern California. The main objectives were 1) to compare the diet between two consecutive years and 2) to examine seasonal variation in the prey items consumed.

Materials and methods

Stomach samples were collected from fish caught in coastal waters off Humboldt Bay (40°46'N, 124°14'W), Trinidad Bay (41°03'N, 124°09'W), and Crescent City (41°46'N, 124°13'W), California (Fig. 1). From May through September 1994, 196 stomachs were collected from Chinook salmon from the three areas. During 1995, 112 stomachs were collected from the same ports but only in June and September. Approximately 60%, 10%, and 30% of the total stomachs collected were taken from Humboldt Bay, Trinidad Bay, and Crescent City, California, respectively, in both years. Stomach collections were obtained from California Department of Fish and Game (CDF&G) port samplers and directly from sportfishermen. Owing to changing and sporadic season opening dates, as well as to varied placement of port samplers and weather conditions, an unbiased random sampling scheme was not possible. All fish were obtained from the recreational fishery and were greater than or equal to 22 inches (≥56 cm), the CDF&G minimum size limit. Total length measurements were obtained for 54 fish in 1994 and ranged from 59 to 96 cm ($\bar{x}$=74 cm). Although no fish were measured in 1995, they were similar in size to those collected in 1994. This finding suggests that all fish sampled were three to five years of age (Healey, 1991).

Manuscript accepted 23 October 1998.
Fish. Bull. 97:717–721 (1999).

Chinook salmon stomach contents were removed from the digestive tract, fixed in 10% formalin, transferred to 40% isopropyl alcohol, and sorted under a dissecting microscope into major taxonomic groups. When possible, stomach contents were identified to species.

The best measure of dietary importance is one where both the number and weight of a food category are recorded (Hyslop, 1980) . Stomach content data were summarized by four methods: 1) numerical, 2) gravimetric, 3) frequency of occurrence, and 4) index of importance. Each food group was enumerated and weighed from each stomach. Wet weight of prey items was measured to the nearest 0.01 g. By using these data, percentage of total number (*%N*), percentage of total weight (*%W*), and percentage frequency of occurrence (*%F*) were calculated for each food group. "Index of importance" (IOI) was calculated for each food group as follows:

$$IOI_a = \frac{100 \times HI_a}{\sum_{a=1}^{n} HI},$$

where HI_a = $\%F_a + \%W_a$ for food group a; and
n = the number of different food groups (Hannah, 1980; Gray et al., 1997).

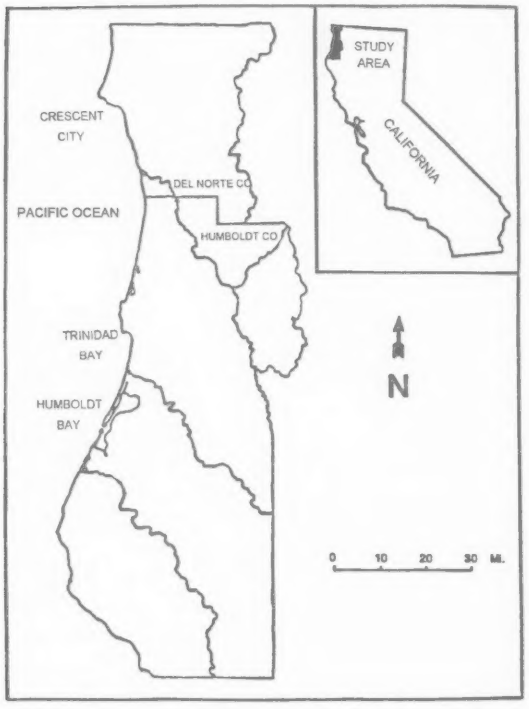


Figure 1
Humboldt Bay, Trinidad Bay, and Crescent City, California.

Because this index calculation is based on *%F* as well as *%W*, the bias towards heavier, infrequently found prey items is reduced.

Results

Values for *%N*, *%F*, *%W*, and *IOI* for prey items encountered in the stomach analyses are listed in Table 1. All stomachs examined (308) contained food items except one from 1994 and two from 1995. Each prey item was present in stomachs sampled from both 1994 and 1995 except for octopi (*Octopus rubescens*) (2), jacksmelt (*Atherinopsis californiensis*) (1), cottids (1), pleuronectids (1), Pacific sandlance (108), and rockfishes (45), which were observed only in 1994 samples and isopods (3) which were present only in 1995 samples. Total values for *%F* did not equal 100% owing to unidentifiable prey items in the diet, especially in 1995 (Table 1).

In 1994, the *IOI* indicated that euphausiids were the predominant food item, accounting for over 27% of the total. Euphausiids not only ranked highest by *%N* and *%F* but also were the leading prey item by *%W*. In addition, notable *IOI* values were observed for crab megalopae, Pacific herring, surf smelt (*Hypomesus pretiosus*), Pacific sandlance, northern anchovy, night smelt (*Spirinchus starksi*), and squid (*Loligo opalescens*). Infrequently encountered prey items included Pacific saury (*Cololabis saira*), rockfishes, amphipods, jacksmelt, octopi, shrimp (mysid), juvenile pleuronectids, and juvenile cottids. In 1995, chinook consumed primarily northern anchovy, which represented over 33% of the total *IOI* but also preyed upon Pacific herring, squid, Pacific saury, surf smelt, night smelt, euphausiids, and crab megalopae. Only rarely were amphipods, isopods, and shrimp found in stomachs. Large interannual variations in *IOI* can be seen for euphausiids, crab megalopae, Pacific sandlance, northern anchovy, squid, and Pacific saury.

Seasonal variation of dominant prey items, for 1994 and 1995, is illustrated in Figure 2, A and B, respectively. In 1994, 88 stomachs were examined from May and June (late spring). *IOI* values for euphausiids (34%), crab megalopae (25%), and Pacific herring (17%) dominated all other prey items. Late summer *IOI* values (based on 108 stomachs acquired in August and September 1994) indicated Pacific sandlance (22%), surf smelt (21%), northern anchovy (17%), and euphausiids (14%) to be major prey items. In 1995, 26 stomachs were examined from fish collected in June and 86 from September. The *IOI* values in our study showed that squid (45%), surf smelt (25%), euphausiids (19%), and Pacific herring (11%) are important prey items in late spring whereas

Table 1

Values for percentages by number (*%N*), frequency (*%F*) and weight (*%W*) for prey items observed in stomachs of chinook salmon, *Oncorhynchus tshawytscha*, collected in the coastal waters off Humboldt Bay, Trinidad Bay, and Crescent City, CA, during the summers of 1994 and 1995.

	1994				1995			
	%N	*%F*	*%W*	*IOI*	*%N*	*%F*	*%W*	*IOI*
Fishes								
Clupea pallasii	0.1	5.6	17.5	12.2	0.5	5.5	17.8	15.7
Engraulis mordax	0.1	3.6	8.7	6.5	8.3	14.6	34.6	33.2
Hypomesus pretiosus	0.1	6.7	12.2	10.0	0.4	2.7	9.6	8.3
Spirinchus starksi	0.2	6.7	4.7	6.0	1.3	2.7	7.0	6.5
Cololabis saira	0.0	1.0	4.3	2.8	1.9	4.6	12.7	11.6
Atherinopsis californiensis	0.0	0.5	0.6	0.6	—	—	—	—
Ammodytes hexapterus	0.4	8.7	9.8	9.8	—	—	—	—
Sebastes spp. (juvenile)[1]	0.2	3.6	1.6	2.7	—	—	—	—
Cottidae	0.0	0.5	0.0	0.3	—	—	—	—
Pleuronectidae	0.0	0.5	0.0	0.3	—	—	—	—
Euphausiid								
Thysanoessa spinifera	71.4	23.1	28.7	27.4	80.8	3.6	5.3	6.0
Crustaceans								
Cancer magister (megalopa)	27.5	19.5	8.6	14.9	2.7	5.5	0.1	3.8
Mysid	0.0	1.0	0.0	0.6	0.1	0.9	0.0	0.6
Amphipoda								
Atylus tridens	0.0	2.1	0.0	1.1	2.6	0.9	0.0	0.6
Isopoda								
Tecticeps convexus, *Synidotea bicuspida* } combined	—	—	—	—	0.2	0.9	0.0	0.6
Cephalopods								
Loligo opalescens	0.1	5.1	3.2	4.4	1.2	6.4	12.9	13.0
Octopus rubescens	0.0	1.0	0.0	0.6	—	—	—	—
Total	100.0	89.2	100.0	100.0	100.0	48.2	100.0	100.0

[1] *Sebastes entomelas, S. mystinus, S. melanops, S. pinniger* (in rank order of abundance).

northern anchovy (49%), Pacific herring (19%), Pacific saury (17%), and night smelt (10%) dominate in late summer.

Discussion

The feeding habits of northern California chinook salmon varied between years and season. This result is consistent with previous studies. Petrovich (1970) found northern anchovy, euphausiids, Pacific herring, osmerids, and rockfishes to be the most important prey items in coastal waters off Humboldt Bay and Trinidad Bay in 1960–1964. As in our study, crab megalopae were especially abundant in one year. In contrast to our results, Petrovich reported rockfishes to be present in 13% of all stomachs from 1960 to 1964, and in terms of frequency of occurrence they ranked third to northern anchovy and euphausiids. We encountered only 45 juvenile rockfishes during our study, all of which came from seven stomachs in the spring of 1994, representing only 2% of all stomachs examined.

Petrovich found relatively few Pacific sandlance and squid, and no Pacific saury in salmon stomachs that he examined. Our study shows that each of these food items contributes significantly to the diet of chinook salmon off Northern California (Fig. 2). Pacific sandlance, although absent in 1995 and only present in small numbers during late spring of 1994, were the major food source (*IOI*=22%) in late summer of 1994. Squid were present in late spring and late summer of both years and greatly outranked (*IOI*=45%) all prey items in late spring 1995. Pacific saury were present in stomachs collected during late summer 1994 (*IOI*=8%) and late summer 1995

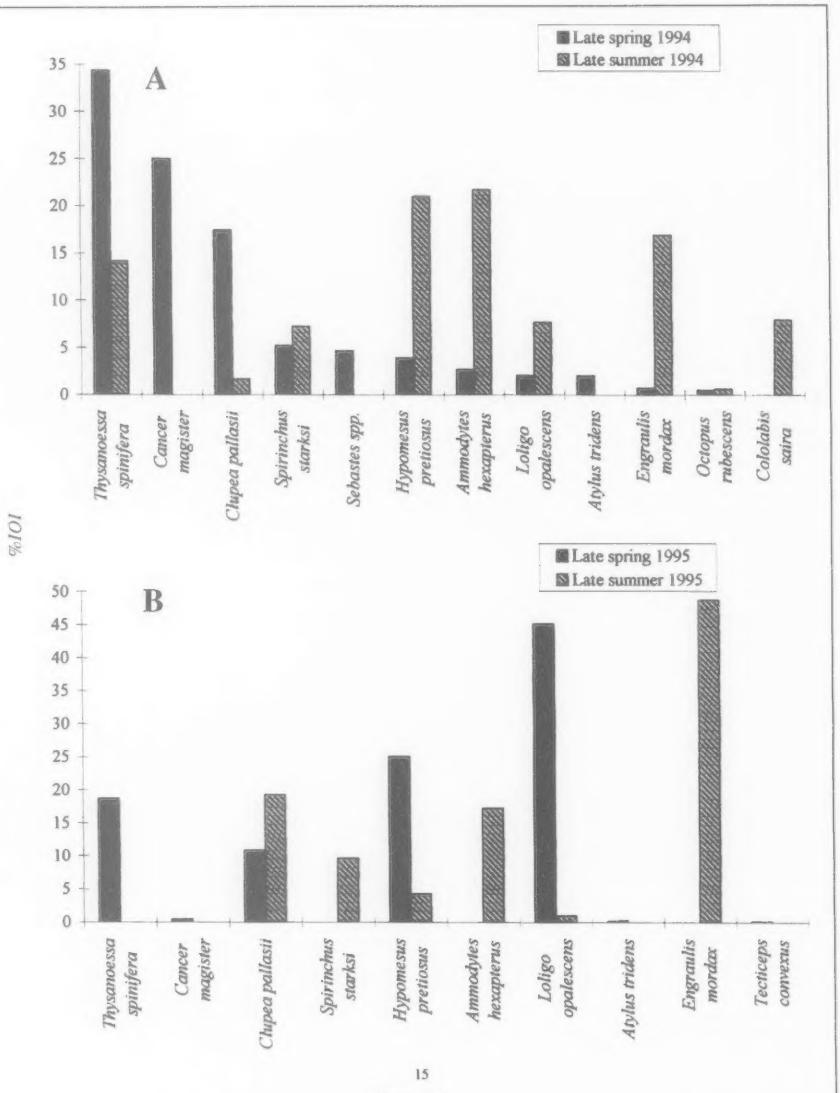


Figure 2

(**A**) 1994 late spring and late summer index of importance (*IOI*) values for predominant prey items consumed by chinook salmon, *Oncorhynchus tshawytscha,* in the coastal waters off Humboldt Bay, Trinidad Bay, and Crescent City, California. (**B**) 1995 late spring and late summer index of importance (*IOI*) values for predominant prey items consumed by chinook salmon, *Oncorhynchus tshawytscha,* in the coastal waters off Humboldt Bay, Trinidad Bay, and Crescent City, California.

(*IOI*=17%). The index of importance indicates that interannual and seasonal variation in the feeding habits of chinook salmon does in fact occur, most likely, in response to variation in the relative abundance of prey along the coast.

Healey (1991) summarized regional trends for coastwide data on chinook feeding habits and recognized that the importance of Pacific herring and Pacific sandlance increased from south to north whereas the importance of rockfishes and northern anchovy decreased. Our data agree with this summary. The diet of chinook salmon off northern California contained characteristic prey items important to chinook found both to the north and south. Although our study

found rockfishes not to be a major prey item of chinook salmon, northern anchovy were in fact commonly taken. In addition, the importance of Pacific herring and Pacific sandlance was substantial. The occurrence of invertebrate prey items (euphausiids, crab megalopae, and squid) during spring months agrees with studies conducted both to the south (Merkel, 1957) and north (Reid, 1961; Prakash, 1962; Brodeur et al., 1987) of the region of our study. Merkel (1957) commonly found euphausiids and squid, April through June, and crab megalopae (presumed to be *Cancer magister*), March through May, in stomachs of fish caught off San Francisco. Similarly, Brodeur et al. (1987), in coastal waters off Oregon and Washington, and Prakash (1962), in British Columbian waters, found euphausiids to be a major prey item during the months of May and June. Prakash also observed an abundance of crab megalopae in chinook diet during June. Squid were a dominant prey item one year in Reid's study off southeastern Alaska during late spring. These results and the great importance of euphausiids, crab megalopae, and squid in our study (Fig. 2) confirm the importance of invertebrate prey, in some years, to chinook salmon.

Acknowledgments

Financial support for this research was provided by the U.S. National Marine Fisheries Service. An earlier version of this manuscript was critically reviewed by R. D. Brodeur.

Literature cited

Bowen , S. H.
1996. Quantitative description of the diet. *In* B. Murphy and D. Willis (eds.), Fisheries techniques, p. 513–532. Am. Fish. Soc. Bethesda, MD, 732 p.

Brodeur, R. D., H. V. Lorz, and W. G. Pearcy.
1987. Food habits and dietary variability of pelagic nekton off Oregon and Washington, 1979–1984. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 57, 32 p.

Brodeur, R.D., and W.G. Pearcy.
1992. Effects of environmental variability on trophic interactions and food web structure in a pelagic upwelling ecosystem. Mar. Ecol. Prog. Ser. Vol. 84:101–119.

Gray, A. E., T. J. Mulligan, and R. W. Hannah.
1997. Food habits, occurrence, and population structure of the bat ray, *Myliobatis californica*, in Humboldt Bay, CA. Environ. Biol. Fish. 49:227–238.

Hannah, R.
1980. Age, growth and food habits of the small mouth bass, *Micropterus dolomieui*, in Clair Eagle Reservoir, CA. Unpubl. M.S. thesis, Humboldt State University, Arcata, CA, 57 p.

Healey, M. C.
1991. Life history of chinook salmon. *In* C. Groot and L. Margolis, (eds.), Pacific salmon life histories, p. 311–393. Univ. British Columbia Press, Vancouver, Canada, 564 p.

Heg, R., and J. Van Hyning.
1951. Food of chinook and silver salmon taken off the Oregon Coast. Oregon Fish Commission Research Briefs 3(2):32–40.

Hyslop, E. J.
1980. Stomach content analysis-a review of methods and their applications. J. Fish Biol. 17:411–429.

Merkel, T. J.
1957. Food habits of king salmon, *Oncorhynchus tshawytscha* (Walbaum), in the vicinity of San Francisco, California. California Fish Game 43(4):249–270.

Miller , D. J., and R. N. Lea.
1972. Guide to coastal marine fishes of California. Calif. Dep. Fish Game Fish Bull. 157:1–249

Nehlsen, W., J. E. Williams, and J. A. Lichatowich.
1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–21.

Pearcy, W. G.
1992. Ecology of North Pacific salmonids. Univ. Washington Press, Seattle, WA, 179 p.

Petrovich, A., Jr.
1970. Biota of near-shore waters off Humboldt Bay and Trinidad Head, 1960–1964, as shown by diet of Pacific Salmon. Unpubl. M.S. thesis, Humboldt State University, Arcata, CA, 69 p.

Prakash, A.
1962. Seasonal changes in feeding of coho and chinook (spring) salmon in southern British Columbia waters. J. Fish. Res. Board Can. 19:851–866.

Pritchard, A. L., and A. L. Tester.
1944. Food of spring and coho salmon in British Columbia. Bull. Fish. Res. Board Can. 65, 23 p.

Reid, G.
1961. Stomach content analysis of troll caught king and coho salmon, southeastern Alaska, 1957–1958. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 379, 8 p.

The development of the digestive tract and eye in larval walleye pollock, *Theragra chalcogramma**

Steven M. Porter

Gail H. Theilacker

Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE, Seattle, Washington 98115
E-mail address (for S. M. Porter): sporter@afsc.noaa.gov

First feeding (FF) is a time at which a fish larva must initiate feeding or face starvation that will weaken it and eventually lead to its death. In most oviparous fish with pelagic eggs, organ systems develop that allow larvae to switch from an internal nutrient source (yolk) to an external source (prey) during the time between hatching and FF. Starvation may be a major cause of the high mortalities that occur during the larval period and thus may affect recruitment (Hjort, 1914; O'Connell, 1980; Theilacker, 1986). Indeed, some studies suggest that recruitment is determined in this period (Houde, 1987; Freeberg et al., 1990).

Laboratory experiments show that at FF, the growth rate of walleye pollock, *Theragra chalcogramma*, larvae decreases (Yamashita and Bailey, 1989), or even ceases for a period (Theilacker and Shen, 1993). Furthermore, delaying the introduction of food at FF causes a reduction of the growth rate and size-at-age (Theilacker and Shen, 1993). These studies indicate that FF walleye pollock lack energy reserves, and thus the availability of nutritious prey at this time is critical. Theilacker and Porter (1995) found that the largest proportion of starving walleye pollock larvae in Shelikof Strait, Gulf of Alaska, are in the size class that includes FF larvae. Thus, the FF period appears to be the time when walleye pollock larvae are most vulnerable to starvation. Studies involving larvae of other marine fish have found similar results (Atlantic mackerel, *Scomber scombrus*, Ware and Lambert, 1985; jack mackerel, *Trachurus symmetricus*, Theilacker, 1986).

Larval walleye pollock survival is dependent upon timely development of organs required for feeding. Of the many developmental changes occurring during the early larval period, two of the most important for walleye pollock may be vision and the digestive tract. Eyesight is probably the most important sense walleye pollock larvae use in finding prey because they are visual predators (Paul, 1983) and do not use chemosensory cues (Davis and Olla, 1995). Digestive tract development is important for efficient assimilation of nutrients needed for growth. In this study, histological sections were used to describe the development of the mouth, digestive tract, and eyes in laboratory-reared walleye pollock, from hatching to 31 days after hatching (DAH), to examine how organs necessary for feeding develop. This is essential to an understanding of why walleye pollock larvae are most vulnerable to starvation during the first week of feeding.

Materials and methods

In 1991 and 1992, adult walleye pollock were collected from Shelikof Strait, Gulf of Alaska, and spawned aboard ship. Fertilized eggs were maintained aboard ship at 3°C for a few days, then transported to the laboratory. In 1991, walleye pollock larvae were reared at Friday Harbor Laboratories, University of Washington, San Juan Island, Washington, and in 1992, at the Alaska Fisheries Science Center, Seattle, Washington. Between 500 and 1000 larvae were reared in a black, circular, 120-L fiberglass tank (62 cm diameter, 43 cm deep) filled with 90 L filtered seawater (salinity=28.0 ±0.5 ppt) and maintained at 6° ±0.5°C, the typical seawater temperature in Shelikof Strait when walleye pollock larvae initiate feeding (Kendall et al., 1987). Larval rearing procedures followed Porter and Theilacker 1996.[1]

Fluorescent fixtures were used with a 16-hour light cycle; the amount of light at the surface of the water in the rearing tank was 17 μ mol photon/m^2/s. Prey consisted of the rotifer *Brachionus plicatilis*, raised on an algal diet of *Isochrysis galbana* and *Pavlova lutheri* high in unsaturated fatty acids (Nichols et al., 1989), as well as of *Acartia* sp. copepod nauplii and copepodites collected from a local lagoon. At 3 DAH, four to five days before FF, rotifers were added at 10/mL and *Acartia* were added at 3/mL to the rearing tank and maintained at this level throughout the rearing

* Contribution 0285-RAO-0 to Fisheries Oceanography Coordinated Investigations (FOCI), NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

[1] Porter, S. M., and G. H. Theilacker. 1996. Larval walleye pollock, *Theragra chalcogramma*, rearing techniques used at the Alaska Fisheries Science Center, Seattle Washington. AFSC processed report 96-06, 26 p. U.S. Dep. Commerce, NOAA, NMFS, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA., 98115.

Manuscript accepted 17 July 1998.
Fish. Bull. 97:722–729 (1999).

period. Eight to 10 larvae were sampled every day or every other day after hatching to 23 DAH in 1991 and to 31 DAH in 1992. Larvae were placed into either Bouin's fixative which was replaced with 70% ethanol 24 to 48 h later, or Z-fix[2] (a solution of 10% formalin with zinc and buffers added). Larvae were dehydrated in a graded series of butyl alcohols, embedded in paraffin wax, sectioned sagittally into 6-µm serial sections, and stained with hematoxylin and eosin (H and E). Standard lengths (SL, tip of upper jaw to end of notocord) of preserved larvae were measured to the nearest 0.08 mm and adjusted to live SL (Theilacker and Porter, 1995). To describe development of the mouth, digestive tract, and eyes, histological sections of 5–10 larvae were examined from each sampling day.

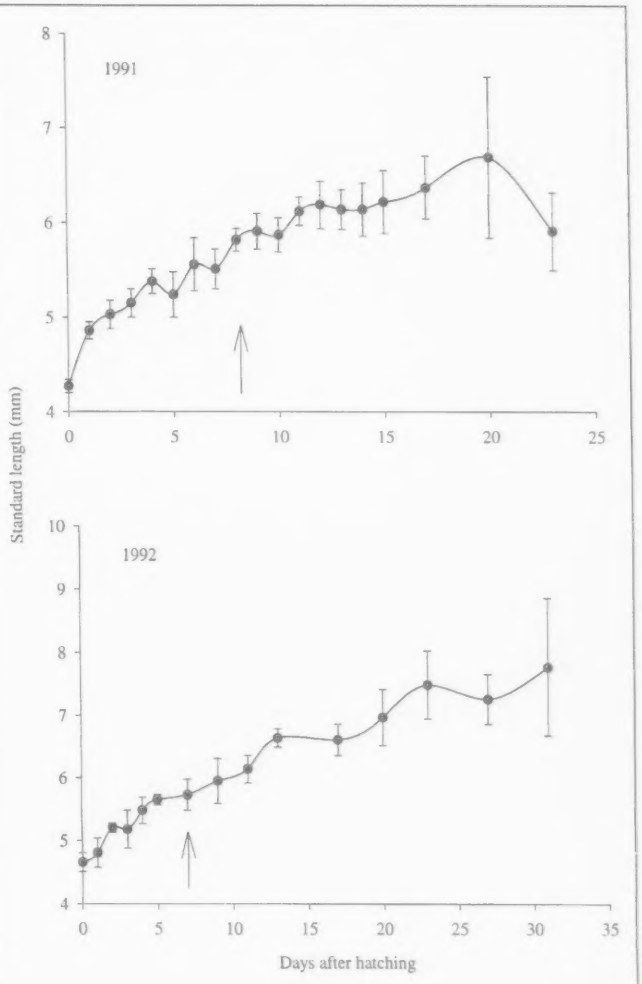


Figure 1

Growth of walleye pollock, *Theragra chalcogramma*, reared at 6°C in the laboratory from hatching to 23 days after hatching in 1991, and to 31 days after hatching in 1992. Mean standard length (preserved length adjusted to live length, see text) and standard deviation are shown; 5 to 10 larvae were measured at each age. The small size for 1991 at 23 days after hatching may be due to sampling slow growing larvae in poor condition (see text). Arrow indicates day of first feeding.

Results

Larval growth

In 1991, the mean SL at hatching was 4.27 ±0.07mm, whereas in 1992 hatching size averaged 4.66 ±0.15mm (Fig. 1). The decrease in average size of larvae sampled on day 23 in 1991 (Fig. 1) was probably due to the sampling of slow growing larvae in poor condition. A bowl was used to sample larvae from the tank, and we suspect that for this sample only slow growing larvae were captured. The overall mean growth rate from hatching to 20 DAH was 0.12 mm/d in both 1991 and 1992. In 1992, experiments continued until 31 DAH and average growth from hatching was 0.10 mm/d. The onset of FF occurred over a period of three days; day of first feeding was defined as the time when 50% of the larvae began feeding. In 1991, day of first feeding occurred at 8 DAH, and the mean SL was 5.82 ±0.12 mm. In 1992, larvae began feeding at 7 DAH, and the mean SL was 5.73 ±0.25 mm (Fig. 1).

Mouth and digestive tract development

At hatching a membrane covered the mouth, and jaw cartilage had not yet formed. At 2 DAH the membrane began to degenerate leaving an orifice that was 22 to 55 µm wide. Mouth and jaw cartilage also began forming at this time, and the cartilage in the roof of the mouth, the trabeculum cranii, became most distinct. All jaw cartilage elements were present and almost completely formed at 5 DAH (approximately 2 days before FF); the mouth was considered functional 5 to 6 DAH (Table 1).

At hatching the gut was a straight tube with a narrow lumen. The foregut could be distinguished

[2] Anatech, Ltd., Battle Creek, MI.

Table 1

Mean standard length (tip of upper jaw to end of notocord) and age at the development of various elements of the mouth, digestive tract, and eye for walleye pollock, *Theragra chalcogramma*, reared at 6°C in the laboratory in 1991 and 1992. '+', vacuoles were not observed at 23 DAH in 1991, the last sampling day. Preserved standard length adjusted to live standard length (Theilacker and Porter, 1995). SD = standard deviation. *n* = number of larvae measured. Age = days after hatching.

	Mean standard length mm (SD)				
	1991	*n*	1992	*n*	Age (year)
Mouth and digestive tract					
Foregut, midgut, and hindgut separated by valves	5.15 (0.15)	5	5.18 (0.30)	5	3 (1991,92)
Jaw developed and mouth functional	5.56 (0.28)	5	5.65 (0.08)	5	5 (1992) 6 (1991)
Folding of midgut epithelium	6.19 (0.25)	5	6.14 (0.22)	10	11 (1992) 12 (1991)
Midgut coiling, eosinic vesicles in the hindgut	6.14 (0.28)	5	6.64 (0.15)	8	13 (1992) 14 (1991)
Lipid vacuoles in midgut	+		7.49 (0.54)	10	23 (1992)
Eye					
Ocular motor muscles apparent	5.15 (0.15)	5	5.18 (0.30)	5	3 (1991,92)
Eye fully pigmented	5.38 (0.13)	5	5.48 (0.21)	5	4 (1991,92)
Lens retractor muscle developed	6.22 (0.33)	5	no samples taken		15 (1991)

by its cuboidal epithelium, but no distinction could be made between the midgut and hindgut which were lined with similar columnar epithelium. At 1 DAH, the gut lumen widened and began to separate into a long midgut and short hindgut that were demarcated by a constriction at the future site of the ileocaecal valve. At 3 DAH, the pyloric valve separated the foregut and midgut, and the ileocaecal valve separated the midgut and hindgut (Table 1; Fig. 2). At 11 to 12 DAH (4 days after FF) the gut began to develop large folds, and began to coil 13 to 14 DAH (6 days after FF) (Table 1). Also, at 13 to 14 DAH, eosinic vesicles (also referred to as eosinophilic granules or inclusions), ranging in size from 1 to 3 μm, began appearing in the apical cytoplasm of the hindgut epithelial cells (Table 1). Vacuoles in midgut epithelial cells were first observed at 23 DAH in 1992 larvae (Table 1). The vacuoles were not distinct and observed only in one larva out of ten. Walleye pollock larvae showed no other changes in gut structure (i.e. no stomach, or pyloric caeca) up to 31 DAH.

Eye development

At hatching, a lens was present, and small scattered patches of pigment were located throughout the retina (Fig. 3). The pigment patches increased in size and joined to form the pigment layer; by 4 DAH the eye was fully pigmented (Table 1). Ocular motor muscles were not developed at hatching, but at 3 DAH these muscles became apparent (Table 1). At 9 DAH, the lens retractor muscle was identified as a thin structure that connected the lens to the retina. From 9 to 15 DAH the muscle increased in width as it grew. The size and shape of this muscle changed very little beyond 15 DAH; therefore it was considered functional beginning at this time (Fig. 4, Table 1).

Discussion

Larval growth

Growth of walleye pollock larvae in this study was similar between years (0.12 mm/d from hatching to 20 DAH for both 1991 and 1992) and to rates found by others for walleye pollock larvae reared at 6°C in the laboratory; 0.14 mm/d from hatching to 19 DAH (Theilacker and Shen, 1993), 0.11 mm/d from hatching to 21 DAH (Yamashita and Bailey, 1989) and 0.065 mm/d from hatching to 15 DAH (Nishimura and Yamada, 1984). Growth was slightly lower than the 0.14 to 0.23 mm/d calculated for field-collected walleye pollock larvae (Bailey et al., 1996).

Mouth and digestive tract

From observations on live larvae, Bailey and Stehr (1986) found that walleye pollock have no mouth at hatching; the mouth begins to develop 2 days later

Figure 2

Walleye pollock, *Theragra chalcogramma*, larva 3 days after hatching. The foregut (FG) and midgut (MG), and midgut and hindgut (HG) are separated by the pyloric and ileocaecal valves respectively (arrowheads). (Bouin's fixative, H and E; standard length=5.24 mm; scale bar=100 µm). Y = yolk.

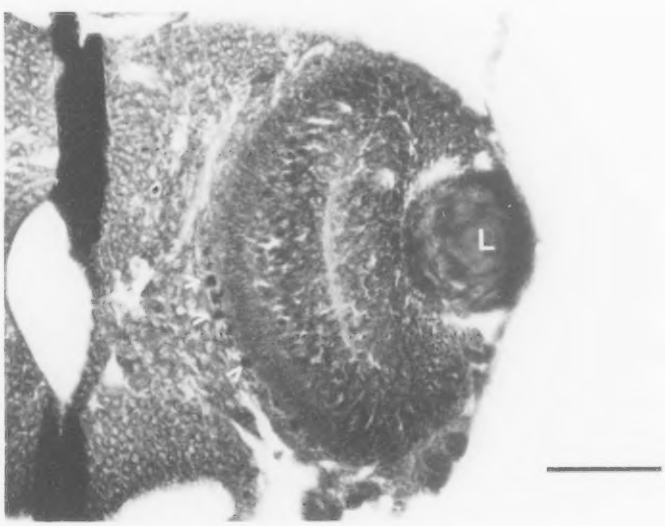


Figure 3

Walleye pollock, *Theragra chalcogramma*, eye at hatching. The eye is not fully pigmented. Arrowheads identify patches of pigment. (Bouin's fixative, H and E; standard length=4.34 mm; scale bar=50 µm). L = lens.

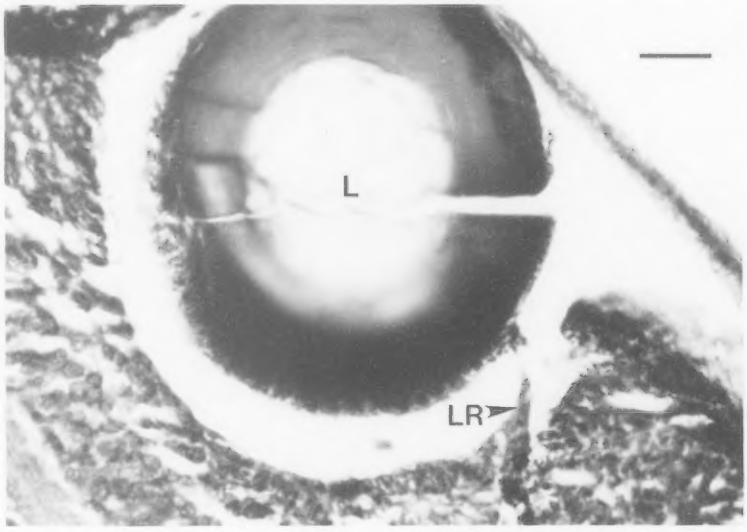


Figure 4

The lens retractor muscle (LR) in the eye of a 15-day posthatching walleye pollock, *Theragra chalcogramma*, larva. (Bouin's fixative, H and E; standard length=6.65 mm; scale bar=20 μm). L = lens.

and is functional by 4 to 5 DAH. Histological analysis in this study showed that mouth and jaw development proceeded at a similar rate; the jaw was fully formed and the mouth was functional 5 to 6 DAH. As in Atlantic cod, *Gadus morhua*, larvae (Kjørsvik et al., 1991), the first feature of the walleye pollock mouth to form was the trabeculum cranii ("roof of the mouth").

At hatching, walleye pollock larvae had a straight-tube gut. This simple gut arrangement has been noted for larvae of other species of fish as well (northern anchovy, *Engraulis mordax*, O'Connell, 1981; Atlantic cod, *G. morhua,* Kjørsvik et al., 1991; turbot, *Scophthalmus maximus,* Segner et al., 1994). At 3 DAH, three distinct portions of the gut could be identified: the foregut, midgut, and hindgut. This gut arrangement is typical of larval fish (Govoni et al., 1986) and walleye pollock larvae showed no major changes in gut structure (i.e. no stomach, or pyloric cæca) up to 31 DAH. For larval fish, major changes in gut structure happen rapidly at metamorphosis rather than gradually during the larval period (Govoni et al., 1986). However, at 11 to 12 DAH (4 days after FF) the larval walleye pollock midgut epithelium began to develop large folds, and the gut began to coil 13 to 14 DAH (6 days after FF). For walleye pollock larvae reared at 6°C, Oozeki and Bailey (1995) noted that gut coiling began on 16 DAH and was complete by day 23. Midgut coiling increases the length of the gut, and the residence time of prey in it (Yamashita and Bailey, 1989). At one week after FF, both epithelial folds and gut coiling enable walleye pollock larvae to assimilate nutrients more efficiently through increased absorptive surface area and longer residence times.

Histological evidence suggests the larval walleye pollock gut functions in the same manner as in other fish larvae. The midgut of fish larvae digests and absorbs lipids (Govoni et al., 1986) and this appears to be the function of the larval walleye pollock midgut as well. For larval whitefish, *Coregonus fera*, lipid vacuoles appear as circular "voids" in the apical portion of the midgut epithelial cells one day after feeding (Loewe and Eckmann, 1988). In other species of fish, similar vacuoles are also reported to contain lipid (goldfish, *Carassius auratus*, Iwai, 1968; turbot, *S. maximus*, Segner et al., 1994). In our study, vacuoles (circular voids) were observed in midgut epithelial cells of one walleye pollock larva at 23 DAH. This is later in development than they have been observed in other fish larvae but lipase is present in walleye pollock larvae at hatching; therefore lipid digestion could occur at FF. Lipase activity increases with age (Oozeki and Bailey, 1995) so that as larvae grow, more lipid can be digested and this could produce larger, more visible (by H and E stain-

ing) vacuoles with age. There was probably lipid in the midgut cells earlier than 23 DAH but in such small amounts so that it could not be identified without special staining. The larval walleye pollock hindgut appears to function in protein digestion like the hindgut of other species of fish larvae (Govoni et al., 1986). Watanabe (1984) demonstrated that protein is pinocytotically moved into hindgut epithelial cells for intracellular digestion. Iwai and Tanaka (1968) stated that the intracellular protein appears as eosinophilic granules (also referred to as eosinophilic vesicles or inclusions) within the apical portion of the hindgut cells. At 13 to 14 DAH (5 to 7 days after FF), eosinic vesicles appear in the apical cytoplasm of the hindgut epithelial cells of walleye pollock larvae. For Atlantic cod, *G. morhua*, larvae (Kjørsvik et al., 1991), a close relative of walleye pollock, inclusions were not observed until 2 to 5 days after FF. In other studies eosinophilic inclusions have been observed soon after FF (northern anchovy, *E. mordax*, O'Connell, 1981; whitefish, *C. fera*, Loewe and Eckmann, 1988; turbot, *S. maximus*, Segner et al., 1994). Trypsin is present in walleye pollock larvae at hatching, its activity increases with age, and it is not supplemented by prey in the gut (Oozeki and Bailey, 1995). Eosinophilic vesicles appeared at the time the gut began to coil, and both coiling and increased trypsin would allow increased digestion of prey making more protein available to the hindgut, possibly explaining why vesicles were not apparent until some time after FF. The appearance of lipid vacuoles and eosinophilic vesicles after the first week of feeding provides evidence for improved digestive capability.

Eye

Sight is probably the most important sense walleye pollock larvae use for feeding. Walleye pollock rely on vision to search for prey (Paul, 1983) and do not respond to chemosensory cues (Davis and Olla, 1995). Laboratory experiments show that a group of walleye pollock larvae, age 21 DAH, remains aggregated when rotifers are introduced into the group, but when only the scent of rotifers is introduced, the group disperses (Davis and Olla, 1995). Because they are visual predators and because light below 0.006 μ mol photon/m^2/s limits their ability to capture prey (Paul, 1983), walleye pollock larvae probably have a pure-cone retina like many other species of fish larvae. Blaxter and Staines (1970) examined the retina of 12 species of fish larvae including haddock, *Melanogrammus aeglefinus* (which belongs to the same family as walleye pollock, Gadidae), they showed that haddock and seven other species have a pure cone retina. Olla and Davis (1990) stated that the retina of walleye pollock larvae most likely does not contain rods. It is unknown when rods begin to appear in walleye pollock, but for herring, *Clupea harengus* (Blaxter and Jones, 1967), plaice, *Pleuronectes platessa* (Blaxter, 1968), and sole, *Solea solea* (Sandy and Blaxter, 1980), rods begin to appear at metamorphosis.

The lack of eye pigmentation at hatching has been found for many teleosts (Blaxter, 1986), including walleye pollock (Bailey and Stehr, 1986; our study), and eyes are probably nonfunctional at this time (Blaxter, 1986). Ocular motor muscles developed just as walleye pollock eyes became fully pigmented (3 DAH). The development of eye pigmentation and ocular motor muscles should provide a FF larva with sight and the ability to move its eyes. The lens retractor muscle did not develop until after FF; it was considered functional beginning at 15 DAH. The lens retractor muscle develops after FF in other species of fish as well (northern anchovy, *E. mordax*, O'Connell, 1981; white seabass, *Atractoscion nobilis*, Margulies, 1989). This muscle allows a larva to focus on objects at different distances, thereby increasing the field of vison (Munz, 1971). Because this muscle was not functional until 15 DAH, for about a week after FF a larval walleye pollock's field of view is restricted because it is unable to change the focus of its eyes. Thereafter, visual acuity improves, allowing walleye pollock larvae to detect both prey and predators more easily.

In Shelikof Strait, Gulf of Alaska, the proportion of starving walleye pollock larvae decreases dramatically after the first week of feeding (Theilacker and Porter, 1995; Theilacker et al., 1996) and the physiological condition of walleye pollock larvae improves as they grow; that is, fewer larvae are found in poor condition (Theilacker et al., 1996). Improvements to vision (the lens retractor muscle) and a combination of morphological changes to the gut (folding and coiling) as well as an increase in digestive enzymes (Oozeki and Bailey, 1995) contribute to walleye pollock larvae becoming less vulnerable to starvation after the first week of feeding. Additional contributing factors may include developmental changes occurring to other organ systems (e.g. development of trunk musculature and lateral line system as has been shown for other species of fish larvae; Blaxter, 1986; O'Connell, 1981), and larvae becoming better predators as they grow. For northern anchovy, *E. mordax*, larvae, feeding success rapidly improves during the first week of feeding (Hunter, 1972). At hatching walleye pollock larvae lack functional eyes and mouth, and have a straight-tube gut; the development of these between hatching and FF allows larvae to begin feeding, and their continued development after FF improves the larvae's chance of survival.

Acknowledgments

We would like to thank the following people for their help: Debbie Blood, Ric Brodeur, Jay Clark, Nazila Merati, and Matt Wilson for spawning walleye pollock and bringing the eggs back to Seattle; Annette Brown and Stella Spring for assistance rearing the larvae; Frank Morado and Linda Cherepow for providing assistance during the histological phase of this study. Kevin Bailey, Art Kendall, Mike Canino, Frank Morado, and anonymous reviewers provided helpful comments on drafts of this manuscript. The University of Washington, Friday Harbor Laboratory, provided aquarium space in 1991.

Literature cited

Bailey, K. M., and C. L. Stehr.
1986. Laboratory studies on the early life history of the walleye pollock, *Theragra chalcogramma* (Pallas). J. Exp. Mar. Biol. Ecol. 99:233–246.

Bailey, K. M., A. L. Brown, M. M. Yoklavich, and K. L. Meir.
1996. Interannual variability in growth of larval and juvenile walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska, 1983–91. Fish. Ocean. 5 (suppl. 1):137– 147.

Blaxter, J. H. S.
1968. Light intensity, vision, and feeding in young plaice. J. Exp. Mar. Biol. Ecol. 2:293–307.
1986. Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. Trans. Am. Fish. Soc. 115:98–114.

Blaxter, J. H. S., and M. P. Jones.
1967. The development of the retina and retinomotor responses in the herring. J. Mar. Biol. Assoc. U. K. 47:677–697.

Blaxter, J. H. S., and M. Staines.
1970. Pure-cone retinae and retinomotor responses in larval teleosts. J. Mar. Biol. Assoc. U. K. 50:449–460.

Davis, M. W., and B. L. Olla.
1995. Formation and maintenance of aggregations in walleye pollock, *Theragra chalcogramma*, larvae under laboratory conditions: role of visual and chemical stimuli. Environ. Biol. Fish. 44:385–392.

Freeberg, M. H., W. W. Taylor, and R. W. Brown.
1990. Effect of egg and larval survival on year-class strength of lake white fish in Grand Traverse Bay, Lake Michigan. Trans. Am. Fish. Soc. 119:92–100.

Govoni, J. J., G. W. Boehlert, and Y. Watanabe.
1986. The physiology of digestion in fish larvae. Environ. Biol. Fishes 16:59–77.

Hjort, J.
1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 20:1–228.

Houde, E. D.
1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2:17–29.

Hunter, J. R.
1972. Swimming and feeding behavior of larval anchovy, *Engraulis Mordax*. Fish. Bull. 70:821–838.

Iwai, T.
1968. The comparative study of the digestive tract of teleost larvae—V. Fat absorption in the gut epithelium of goldfish larvae. Bull. Jpn. Soc. Sci. Fish. 34:973–978.

Iwai, T., and M. Tanaka.
1968. The comparative study of the digestive tract of teleost larvae—III. Epithelial cells in the posterior gut of halfbeak larvae. Bull. Jpn. Soc. Sci. Fish. 34:44–48.

Kendall, A. W., Jr., M. E. Clarke, M. M. Yoklavich, and G. W. Boehlert.
1987. Distribution, feeding, and growth of larval walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. Fish. Bull. 85:499–521.

Kjørsvik, E., T. Van Der Meeren, H. Kryvi, J. Arnfinnson, and P.G. Kvenseth.
1991. Early development of the digestive tract of cod larvae, *Gadus morhua*, during start- feeding and starvation. J. Fish Biol. 38:1–15.

Loewe, H., and R. Eckmann.
1988. The ontogeny of the alimentary tract of coregonid larvae: normal development. J. Fish Biol. 33:841–850.

Margulies, D.
1989. Size-specific vulnerability to predation and sensory system development of white seabass, *Atratoscion nobilis*, larvae. Fish. Bull. 87:537–552.

Munz, F.W.
1971. Vision: visual pigments. *In* W. S. Hoar, and D. J. Randall (eds.), Fish physiology, vol. 5, Sensory systems and electric organs, p. 1–8. Academic Press, New York, NY.

Nichols, P. D., D. G. Holdsworth, J. K. Volkman, M. Daintith, and S. Allanson.
1989. High incorporation of essential fatty acids by the rotifer *Brachionus plicatilis* fed on the prymnesiophyte *Pavlova lutheri*. J. Mar. Freshwater Res. 40:645–655.

Nishimura, A., and J. Yamada.
1984. Age and growth of larval and juvenile walleye pollock, *Theragra chalcogramma* (Pallas), as determined by otolith daily growth increments. J. Exp. Mar. Biol. Ecol. 82:191–205.

O'Connell, C. P.
1980. Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods. Fish. Bull. 78:475–489.
1981. Development of organ systems in the northern anchovy, *Engraulis mordax*, and other teleosts. Am. Zool. 21:429–446.

Olla, B. L., and M. W. Davis.
1990. Effects of physical factors on the vertical distribution of larval walleye pollock *Theragra chalcogramma* under controlled laboratory conditions. Mar. Ecol. Prog. Ser. 63:105–112.

Oozeki, Y., and K. M. Bailey.
1995. Ontogenetic development of digestive enzyme activities in larval walleye pollock, *Theragra chalcogramma*. Mar. Biol. 122:177–186.

Paul, A. J.
1983. Light, temperature, nauplii concentrations, and prey capture by first feeding pollock larvae *Theragra chalcogramma*. Mar. Ecol. Prog. Ser. 13:175–179.

Sandy, J. M., and J. H. S. Blaxter.
1980. A study of retinal development in larval herring and sole. J. Mar. Biol. Assoc. U.K. 60:59–71.

Segner, H., V. Storch, M. Reinecke, W. Kloas, and W. Hanke.
1994. The development of functional digestive and metabolic organs in turbot, *Scophthalmus maximus*. Mar. Biol. 119:471–486.

Theilacker, G. H.
1986. Starvation-induced mortality of young sea-caught jack

mackeral, *Trachurus symmetricus*, determined with histological and morphological methods. Fish. Bull. 84:1–17.

Theilacker, G. H., K. M. Bailey, M. F. Canino, and S. M. Porter.
1996. Variations in larval walleye pollock feeding and condition: a synthesis. Fish. Ocean. 5 (suppl. 1):112–123.

Theilacker, G. H., and S. M. Porter.
1995. Condition of larval walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska assessed with histological and shrinkage indices. Fish. Bull. 93:333–344.

Theilacker, G. H., and W. Shen.
1993. Calibrating starvation-induced stress in larval fish using flow cytometry. Am. Fish. Soc. Symp. 14:85–94.

Ware, D. M., and, T. C. Lambert.
1985. Early life history of Atlantic mackerel (*Scomber scombrus*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 42:577–592.

Watanabe, Y.
1984. An ultrastructural study of intracellular digestion of horseradish peroxidase by the rectal epithelial cells in larvae of a freshwater cottid fish *Cottus noawae*. Bull. Jpn. Soc. Sci. Fish. 50:409–416.

Yamashita, Y., and K. M. Bailey.
1989. A laboratory study of the bioenergetics of larval walleye pollock, *Theragra chalcogramma*. Fish. Bull. 87:525–536.

Evaluation of small T-anchor and dart tags for use in marking hatchery-reared juvenile red drum, *Sciaenops ocellatus*

Brent L. Winner

Robert H. McMichael Jr.

Laurel L. Brant

Florida Marine Research Institute
Florida Department of Environmental Protection
100 Eighth Avenue SE, St. Petersburg, Florida 33701-5095
E-mail address (For B. L. Winner): Winner_B@epic7.dep.State.fl.us

Red drum, *Sciaenops ocellatus*, is an estuary-dependent marine species found in coastal and nearshore waters in the western Atlantic Ocean from Maine to Florida and in the Gulf of Mexico from Florida to Vera Cruz, Mexico (Yokel, 1966, 1980). Red drum are highly sought after as food and gamefish. Annual commercial landings in Florida averaged nearly 1.0 million pounds from the early 1960s until 1986, when the sale of red drum was prohibited. Recreational fishing effort directed toward red drum in Florida has more than doubled since 1989 on both the Atlantic and Gulf coasts (Murphy[1]). Increased fishing pressure on red drum stocks has led to the implementation of various management strategies, such as closing the commercial fishery and reducing the recreational catch by means of bag limits, size limits, and closed seasons. In the 1970s, methods were developed for culturing red drum in controlled hatchery environments, providing a pathway for the use of stock enhancement for managing the fishery (Arnold et al., 1977; Roberts et al., 1978a, 1978b). Red drum stock enhancement has been conducted extensively in Texas and, to a lesser degree, in Florida and South Carolina (Matlock et al., 1986; Willis et al., 1995; Smith et al.[2]).

Monitoring stocked fish populations in the wild is critical in determining the impact of stocked fish on the fishery and the natural population. Red drum are stocked at various sizes: (phase-1 (25–50 mm SL); phase-2 (50–100 mm SL); and phase-3 (100–200 mm)). Stocking larger size red drum (phase-2 or -3), facilitates the use of tagging as a method of tracking these fish in the wild. Tagged fish can provide valuable data on stock identity, fishing pressure, movements, abundance, age and growth, mortality, and stocking-program success (Ricker, 1956; Hilborn et al., 1990; McFarlane et al., 1990). However, the usefulness of these data depends on knowledge of tag-retention rates and of the effects of tagging on fish growth and survival.

A variety of tag types have been tested on red drum of various sizes. Several studies have evaluated the use of coded wire tags in juvenile red drum (phase-2, 50–100 mm SL, Bumguardner et al., 1990, 1992; Szedlmayer and Howe, 1995). Because coded wire tags are not externally visible, recreational and commercial fishermen are not likely to see them and therefore are not likely to submit capture data to authorities; externally visible tags are better suited for obtaining capture information from recreational and commercial fishermen.

Externally visible tags are typically restricted to use in red drum larger than 100 mm (phase-3 fish). Retention of externally visible tags in phase-3 red drum (100–200 mm SL) has not been rigorously tested, and little is known of the effects of these tags on survival or growth in this size of red drum. Some studies have tested the effects of various external tags on large red drum (>300 mm SL; Elam, 1971; Weaver, 1976; Hein and Shepard, 1980a; Gutherz et al., 1990). Matlock et al. (1984) reported using Monel jaw tags and Willis et al. (1995) reported using internal-anchor tags in fingerling red drum (100–200 mm SL), but neither report addressed tag-retention rates or effects of tags on growth or survival.

The Florida Department of Environmental Protection's Stock Enhancement and Research Facility (SERF) has the capability of rearing phase-1, -2, and -3 red drum for release. Data from this study were used to evaluate the efficacy of two types of external tags in hatchery-reared phase-3 juvenile red drum, and to provide tag-retention and survival estimates, which are necessary for correctly interpreting capture information.

Materials and methods

Retention of T-anchor and dart tags in hatchery-reared red drum (102–173 mm SL) was evaluated over a 423-day period. Mortality associ-

[1] Murphy, M. D. 1994. A stock assessment for red drum, *Sciaenops ocellatus*, in Florida. Florida Marine Research Institute. Report to the Fla. Mar. Fish. Comm., Tallahassee, FL, 28 p.

[2] Smith T. I. J., M. R. Denson, D. B. White, and W. E. Jenkins. 1993. Evaluation of a preliminary red drum stock enhancement program in South Carolina. SC Wildl. Mar. Res. Dep., Mar. Resour. Res. Inst. Annu. Performance Rep. Charleston, SC, 21 p.

Manuscript accepted 16 September 1998.
Fish. Bull. 97:730–735 (1999).

ated with tagging was monitored for the first 111 days of the experiment.

T-anchor tags (IEX tags[3], Fig. 1) had an 18-mm "T" with molded polyethylene on both sides for support. Attached to the "T" portion of the tag was a 42-mm streamer, the distal two-thirds of which was encased in polyethylene. T-anchors were inserted through a 1-mm-diameter hole made with a pointed, stainless-steel rod. Tags were inserted on the left ventral side of the fish near the distal end of the pelvic fin. Once inserted, the tag streamer was pulled so that the T-anchor rested along the body cavity wall, with the streamer protruding.

Dart tags (PDX tags[2], Fig. 1) had a 9-mm, semi-rigid plastic barb attached to a 45-mm plastic streamer that was encased in polyethylene. Dart tags were inserted into the pterygiophores of the spinous dorsal fin by using a stainless-steel canula.

We dipped all tags and applicators in Betadyne before tagging each fish to minimize the possibility of infection. The streamer of each tag was imprinted with a unique tag number so that we could identify individual specimens.

All red drum used in this experiment were spawned and maintained in ponds at the Florida Department of Environmental Protection's Stock Enhancement Research Facility (SERF) in Port Manatee, Florida. The holding ponds were drained at 290 days after spawning and fish were dip-netted to a small holding tank, where they were anesthetized (Tricaine menthanesulphonate, MS222, 100 ppm). Fish were measured (SL mm) and randomly assigned to one of three treatment groups: dart tagged, T-anchor tagged, and controls (handled but not tagged). Each treatment group contained 100 fish (mean SL=140 mm, mean weight=40 g), divided equally between two 1.5-m-diameter net pens with a volume of 2.12 m^3. Net pens were constructed of 6.25-mm knotless nylon mesh and were submerged within a closed aquarium system (>79,000 liters) with supporting aeration, bio-filter, and rapid sand filter. Salinity (‰), dissolved oxygen (mg/L), and temperature (°C) were monitored daily. Ammonia concentration (NH_3^+, mg/L) was monitored periodically. Fish were fed a combination of cut squid and commercially prepared pelletized fish food at a rate of 2–5% of body weight per day.

Net pens were checked daily for fish mortalities and shed tags. Standard length (SL mm), date, tag type, tag number, and pen number were recorded for all fish mortalities. At 66, 111, and 423 days after tagging (DAT), fish from all net pens were measured (SL mm), tag numbers checked, and tag wounds observed for degree of healing (wound open or closed). Control fish were removed from the study at 111 DAT. We continued to monitor tagged fish from 111 to 423 DAT so that we could evaluate long-term tag retention. All fish were treated for *Amyloodinium* sp. and parasitic copepods at 21 DAT.

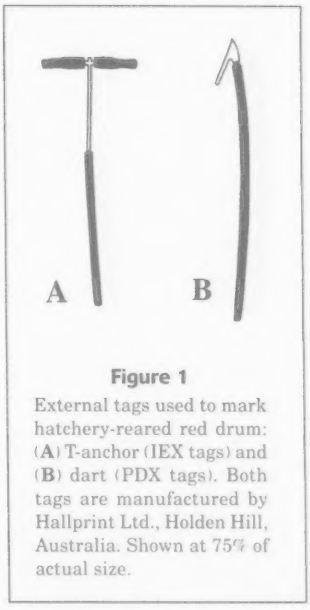


Figure 1
External tags used to mark hatchery-reared red drum: (**A**) T-anchor (IEX tags) and (**B**) dart (PDX tags). Both tags are manufactured by Hallprint Ltd., Holden Hill, Australia. Shown at 75% of actual size.

Standard length measurements of red drum were compared between net pens at 0, 66, and 111 DAT by using a nonparametric Kruskal-Wallis one-way ANOVA on ranks test (α=0.05). Instantaneous survival rates of red drum were compared between treatments by using a two-way (% of fish alive) repeated measures ANOVA (α=0.05) on arcsine-transformed data. Net pen was used as the subject, with tag type as a group factor and days as a level factor (Fox et al., 1995).

Results and discussion

Tag-retention rates in red drum in this study were similar for both T-anchor and dart-tagged fish (Table 1). Average retention rates for T-anchor and dart tags were, respectively, 98% and 99% at 66 DAT; 97% and 95% at 111 DAT; 91% and 89% at 423 DAT. No tags were shed until 41 DAT, and nearly all shedding stopped by 150 DAT (Fig. 2). Both tag types were retained in some red drum as large as 485 mm SL. Wallin et al. (1997) also reported high short-term (30 days) retention rates (100%) of T-anchor tags in ju-

[3] Hallprint Ltd., 27 Jacobsen Crescent, Holden Hill, South Australia 5088, Australia.

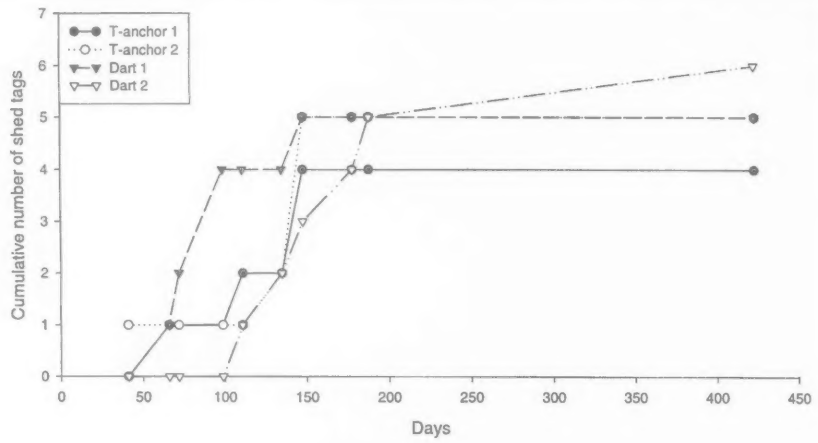


Figure 2

Cumulative number of tags shed by hatchery-reared red drum over a 423-day period. Each tag type was tested in two separate mesh-net pens, each holding 50 fish at start of test.

venile *Centropomus undecimalis*. Collins et al. (1994) found that T-anchor tags had higher long-term retention rates than did dart tags in juvenile *Acipenser brevirostrum* (T-anchor: 92% at 306 DAT; Dart: 50% at 154 DAT). The low retention rates of dart tags in their study may be explained by the fact that the posterior position of the dorsal fin in these fish subjected the tags to the constant motion of the caudal fin and thus enlarged the wound around the tag insertion point (Collins et al., 1994).

Compared with other external tags, T-anchor and dart tags appear to have superior retention rates in small red drum (<380 mm SL). Floy dorsal, Monel metal operculum, Monel metal jaw, Petersen operculum, Petersen dorsal, streamer dorsal, and Carlin dangler tags all yielded lower retention rates (<50% after 154 DAT, Hein and Shepard, 1980a) than did the T-anchor and dart tags tested in this study.

At 66 and 111 DAT, none of the T-anchor tag wounds had healed. Other studies have also shown that tag rotation and movement irritated the incision site, inhibited healing, and left an opening into the body cavity (Smith et al., 1990; Collins et al., 1994). Wallin et al. (1997) suggested that long-term retention of T-anchor tags may be reduced because of the open tag wounds; this was not observed in the 423 days of our study. The anchor portion of some of the T-anchor tags protruded through a hole in the abdominal wall that was separate from the tag insertion point. This may have been an early stage of tag shedding, although it was never verified that the protruding tags were actually shed. Similar results have also been reported in studies with disk-type internal-anchor tags (Vogelbein and Overstreet, 1987; Mattson et al., 1990).

All dart-tag wounds appeared to be healed by 66 DAT. Increases in fish body size during the course of the study caused the streamer portion of some dart tags to become engulfed by the body-wall tissue. This made the tags difficult to detect and impossible to read without dissection. A longer tag streamer could minimize this effect, but it could increase stress on smaller fish during tagging. Simmons and Breuer (1982) also reported tissue growth over tags, which reduced the ability to identify tagged red drum.

Tagging did not appear to adversely affect red drum survival. There was no significant difference in instantaneous survival estimates between treatments (F=2.2, P=0.26). Mean percent survival of control, T-anchor, and dart-tagged fish was, respectively, 79%, 68%, and 79% at 66 DAT and was 67%, 65%, and 77% at 111 DAT (Table 1). Nearly all mortality occurred during the first 40 days of the experiment; 67% of all T-anchor and 83% of all dart-tag mortalities occurred during this time period (Fig. 3). These results are consistent with those of other studies in which these tag types were used (Collins et al., 1994; Szedlmayer and Howe, 1995; Wallin et al., 1997).

Initial lengths of red drum were not significantly different between treatments (H=3.1, P=0.68, df=5, Table 1). Red drum lengths at 66 and 111 DAT were also not significantly different between treatments (66 DAT: H=3.9, P=0.56, df=5; 111 DAT: H=6.4, P=0.27, df=5), suggesting that tagging did not ad-

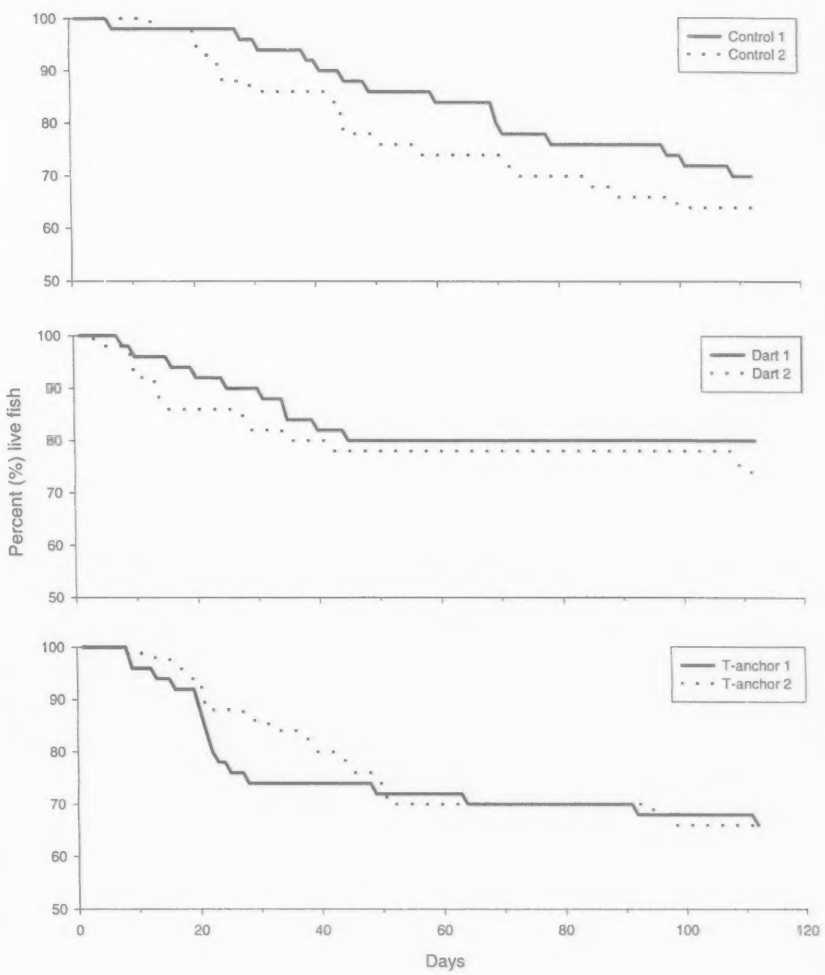


Figure 3
Survival of red drum in each treatment group during the first 112 days of the study.

versely affect fish growth. It is important that a tagging method not affect growth (Ricker, 1956; Wydoski and Emery, 1983), especially when tagging is being used to verify aging methods (e.g. oxytetracycline injection) or to estimate survival rates in the wild (Green et al., 1985; McFarlane et al., 1990). Growth-rate estimates of red drum in our study (0.41–0.50 mm/day) were lower than those for this size of red drum reported in other studies (Colura and Hysmith, 1975; Hein and Shepard, 1980b), possibly because of the high stocking densities in the net pens.

In summary, dart and T-anchor tags are well suited for marking juvenile phase-3 red drum (102–173 mm SL) and are usually retained until the fish are large enough to enter the fishery (Florida minimum size limit for red drum is 368 mm SL). Both tag types were easy to apply and did not affect red drum growth or survival. Although tag retention, survival, and growth rates did not differ between tag types, our results did reveal some potential problems associated with the long-term use of T-anchor tags. The wound around the insertion point of the T-anchor tags did not heal during the 423 days of our experiment, and late in the study, some tags showed signs of expulsion (anchor protrusion through abdominal wall). Both tag types could be used to track releases of

Table 1

Cumulative percent red drum survival (66 and 111 days after tagging (DAT) and tag retention (66, 111, and 423 DAT) for all treatments. Each treatment was replicated in two separate mesh-net pens, each of which held 50 hatchery-reared red drum. Mean standard lengths (mm) and associated standard errors (in parentheses) are also listed for 0, 66, and 111 DAT.

		% Survival DAT		% Tag retention DAT			Mean standard length, mm (standard error) DAT		
Treatment/Pen#		66	111	66	111	423	0	66	111
Control	1	84	50	—	—	—	140 (2.21)	166 (2.87)	195 (3.65)
	2	74	64	—	—	—	136 (2.12)	160 (3.13)	191 (3.23)
T-anchor	3	70	66	98	96	92	138 (1.57)	167 (2.60)	191 (3.05)
	6	66	64	98	98	90	141 (1.88)	163 (2.68)	188 (3.91)
Dart	4	80	80	98	92	90	140 (1.84)	165 (2.70)	184 (3.71)
	5	78	74	100	98	88	138 (1.60)	161 (2.22)	184 (2.28)

hatchery-reared phase-3 red drum and thus allow scientists to monitor and accurately determine the effects such releases have on naturally occurring stocks.

Acknowledgments

We would like thank members of the Stock Enhancement and Aquaculture Development team at Port Manatee, Florida, for providing us with the experimental fish, aquarium facilities, and expert advice and support that made this study possible. We offer special thanks to Victor Neugebauer for his work maintaining aquarium systems and for feeding and checking fish. We thank Llyn French for her art work and help formatting the manuscript. We also thank Judy Leiby, Jim Quinn, John Ransier, Greg Vermeer, and Julie Wallin for providing helpful comments on the manuscript. This project was funded in part by the Department of the Interior, U.S. Fish and Wildlife Service Federal Aid for sportfish Restoration, Project F-43 to the Florida Department of Environmental Protection's Florida Marine Research Institute, and by State of Florida Recreational Saltwater Fishing License funds.

Literature cited

Arnold, C. R., W. H. Bailey, T. D. Williams, A. Johnson, and J. L. Lasswell.
1977. Laboratory spawning and larval rearing of red drum and southern flounder. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 31:437–440.

Bumguardner, B. W., R. L. Colura, A. F. Maciorowski, and G. C. Matlock.
1990. Tag retention, survival, and growth of red drum fingerlings marked with coded wire tags. Am. Fish. Soc. Symp. 7:286–292.

Bumguardner, B. W., R. L. Colura, and G. C. Matlock.
1992. Long-term coded wire tag retention in juvenile *Sciaenops ocellatus*. Fish. Bull. 90:390–394.

Collins, M. R., T. I. J. Smith, and L. D. Heyward.
1994. Effectiveness of six methods of marking juvenile shortnose sturgeons. Prog. Fish-Cult. 56:250–254.

Colura, B., and B. Hysmith.
1975. Fingerling production of spotted seatrout, *Cynoscion nebulosus*, and red drum, *Sciaenops ocellatus*, in saltwater ponds. Tex. Parks Wildl. Dep. Job Completion Rep. (1975).

Elam, L.
1971. Evaluation of fish tagging methods. Tex. Parks Wildl. Coastal Fish. Proj. Rep., p. 39–56.

Fox, E., K. Shotton, and C. Ulrich.
1995. SigmaStat users guide, version 2.0, for Windows. Jandel Scientific, San Rafael, CA, 800 p.

Green, A. W., H. R. Osburn, G. C. Matlock, and H. E. Hegen.
1985. Estimated survival rates for immature red drum in northwest Gulf of Mexico bays. Fish. Res. 3:263–277.

Gutherz, E. J., B. A. Rohr, and R. V. Minton.
1990. Use of hydroscopic molded nylon dart and internal anchor tags on red drum. Am. Fish. Soc. Symp. 7:152–160.

Hein, S. H., and J. A. Shepard.
1980a. A preliminary tagging study on red drum, *Sciaenops ocellatus*, in quarter-acre ponds. *In* Contributions of the Marine Research Laboratory, 1978, p. 33–39. La. Dep. Wildl. Fish. Tech. Bull. 31, Grand Terre Island.

Hein, S. H., and J. A. Shepard.
1980b. Growth of juvenile red drum, *Sciaenops ocellatus*, in quarter-acre ponds. *In* Contributions of the Marine Research Laboratory, 1978, p. 85. La. Dep. Wildl. Fish. Tech. Bull. 31, Grand Terre Island.

Hilborn, R., C. J. Walters, and D. B. Jester Jr.
1990. Value of fish marking in fisheries management. Am. Fish. Soc. Symp. 7:5–7.

Matlock, G. C., B. T. Hysmith, and R. L. Colura.
1984. Returns of tagged red drum stocked into Matagorda Bay, Texas. Tex. Parks Wildl. Manage. Data Ser. 63, 6 p.

Matlock, G. C., R. J. Kemp Jr., and T. J. Heffernan.
1986. Stocking as a management tool for a red drum fishery, a preliminary evaluation. Tex. Parks Wildl. Coastal Fish. Branch Manage. Data Ser. 75, Austin, TX, 27 p.

Mattson, M. T., J. R. Waldman, D. J. Dunning, and Q. E. Ross.
1990. Abrasion and protrusion of internal anchor tags in Hudson River striped bass. Am. Fish. Soc. Symp. 7:121–126.

McFarlane, G. A., R. S. Wydoski, and E. D. Prince.
1990. External tags and marks. Am. Fish. Soc. Symp. 7: 9–29.

Ricker, W. E.
1956. Uses of marking animals in ecological studies: the marking of fish. Ecology 37:665-670.

Roberts, D. E., Jr., B. V. Harpster, and G. E. Henderson.
1978a. Conditioning andinduced spawning of the red drum (*Sciaenops ocellatus*) under varied conditions of photoperiod and temperature. Proc. World Maricult. Soc. 9:311–332.

Roberts, D. E., Jr., L. A. Morey III, G. E. Henderson, and K. R. Halscott.
1978b. The effects of delayed feeding, stocking density, and food density on survival, growth, and production of larval red drum (*Sciaenops ocellatus*). Proc. World Maricult. Soc. 9:333–343.

Simmons , E. G., and J. P. Breuer.
1982. Fish tagging on the Texas coast. Tex. Parks Wildl. Dep. Coastal Fish. Proj. Rep., p. 66–107.

Smith, T. I. J., S. D. Lamprecht, and J. W. Hall.
1990. Evaluation of tagging techniques for shortnose sturgeon and Atlantic sturgeon. Am. Fish. Soc. Symp. 7:134–141.

Szedlmayer, S. T., and J. C. Howe.
1995. An evaluation of six marking methods for age-0 red drum, *Sciaenops ocellatus*. Fish. Bull. 93:191–195.

Vogelbein, W. K., and R. M. Overstreet.
1987. Histopathology of the internal anchor tag in spot and spotted seatrout. Trans. Am. Fish. Soc. 116:745–756.

Wallin, J. E., J. M. Ransier, S. Fox, and R. H. McMichael Jr.
1997. Short-term retention of coded wire and internal anchor tags in juvenile common snook, *Centropomus undecimalis*. Fish. Bull. 95:873–878.

Weaver, J. E.
1976. Retention of floy tag in red drum, black drum, and sheepshead. Tex. Parks Wildl. Dep. Coastal Fish. Proj. Rep., p. 59–65.

Willis, S. A., W. W. Falls, C. W. Dennis, D. E. Roberts, and P. G. Whitchurch.
1995. Assessment of season of release and size at release on recapture rates of hatchery-reared red drum. Am. Fish. Soc. Symp. 15:354–365.

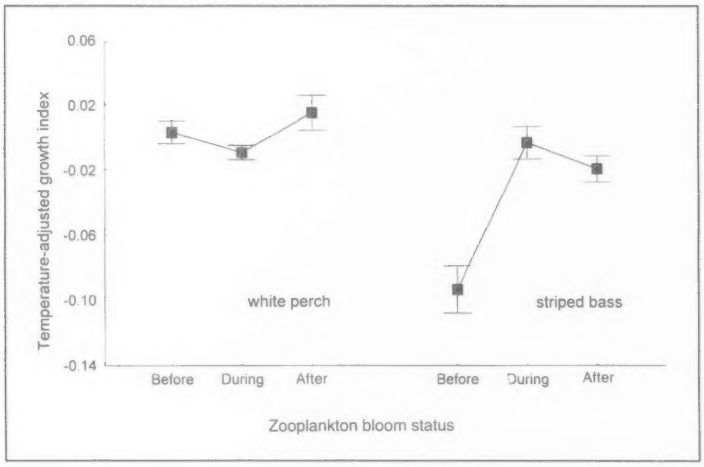
Wydoski, R. S. and L. Emery.
1983. Tagging and marking. *In* L. Nielsen and D. Johnson (eds.), Fisheries techniques, p. 215–237. Am. Fish. Soc., Bethesda, Maryland.

Yokel, B. J.
1966. A contribution to the biology and distribution of the red drum, *Sciaenops ocellata*. M.S. thesis, Univ. Miami, Coral Gables, FL, 160 p.
1980. A contribution to the biology and distribution of the red drum,*Sciaenops ocellata*. *In* R. O. Williams, J. E. Weaver, and F. A. Kalber (eds.), Proceedings of the colloquium on biology and management of red drum and sea trout, Oct. 19–20, 1978, p. 5. Sponsored by Gulf States Mar. Fish. Comm., Ocean Springs, MS [abstract].

Erratum

Erratum: Fishery Bulletin 97(1):80–91
Limburg, Karin E., Michael L. Pace, and Kristin K. Arend
Growth, mortality, and recruitment of larval *Morone* spp. in relation to food availability and temperature in the Hudson River

Correction: Karin Limburg has pointed out that the graphs in Figure 2 (p. 85) were mislabeled. Please find below the correct graphs for white perch and striped bass.



Superintendent of Documents **Publications** Order Form

*5178

☐ **YES,** please send me the following publications:

____ Subscriptions to *Fishery Bulletin*
for $43.00 per year ($53.75 foreign)

The total cost of my order is $ _____ . Prices include regular domestic postage and handling and are subject to change.

_____
(Company or Personal Name) (Please type or print)

_____
(Additional address/attention line)

_____
(Street address)

_____
(City, State, ZIP Code)

_____
(Daytime phone including area code)

_____
(Purchase Order No.)

Charge your order. IT'S EASY!

MasterCard VISA

P3S

Please Choose Method of Payment:

☐ Check Payable to the Superintendent of Documents
☐ GPO Deposit Account ☐☐☐☐☐☐☐–☐
☐ VISA or MasterCard Account
☐☐☐☐☐☐☐☐☐☐☐☐☐☐☐☐
☐☐☐☐ (Credit card expiration date)

To fax your orders (202) 512-2250

_____
(Authorizing Signature)

Mail To: Superintendent of Documents
P.O. Box 371954, Pittsburgh, PA 15250-7954

Thank you for your order!

Fishery Bulletin

Guide for Contributors

Content

Articles published in *Fishery Bulletin* describe original research in fishery marine science, engineering and economics, and the environmental and ecological sciences, including modeling. Articles may range from relatively short to extensive.

Notes are reports of 5 to 10 pages without an abstract and describing methods or results not supported by a large body of data.

Although all contributions are subject to peer review, responsibility for the contents of papers rests upon the authors and not upon the editor or the publisher. It is therefore important that the contents of the manuscript are carefully considered by the authors.

Submission of an article is understood to imply that the article is original and is not being considered for publication elsewhere. Manuscripts should be written in English. Authors whose native language is not English are strongly advised to have their manuscripts checked by English-speaking colleagues prior to submission.

Preparation

Title page should include authors' full names and mailing addresses, the corresponding author's telephone, FAX number, and e-mail address, and a list of key words to describe the contents of the manuscript.

Abstract should not exceed one double-spaced typed page. It should state the main scope of the research but emphasize its conclusions and relevant findings. Because abstracts are circulated by abstracting agencies, it is important that they represent the research clearly and concisely.

Text must be typed double-spaced throughout. A brief introduction should portray the broad significance of the paper; the remainder of the paper should be divided into the following sections: **Materials and methods, Results, Discussion** (or **Conclusions**), and **Acknowledgments**. Headings within each section must be short, reflect a logical sequence, and follow the rules of multiple subdivision (i.e. there can be no subdivision without at least two items). The entire text should be intelligible to interdisciplinary readers; therefore, all acronyms, abbreviations, and technical terms should be spelled out the first time they are mentioned. The scientific names of species must be written out the first time they are mentioned; subsequent mention of scientific names may be abbreviated. Follow *Scientific Style and Format: the CBE Manual for Authors, Editors, and Publishers* (6th ed.), for editorial style, and the most current issue of the American Fisheries Society's *Common and Scientific Names of Fishes from the United States and Canada*, for fish nomenclature. Dates should be written as follows: 11 November 1991. Measurements should be expressed in metric units, e.g. metric tons as t; if other units of measurement are used, please make this fact explicit to the reader. The numeral one (1) should be typed as a one, not as a lower-case el (l). Use of appendices is discouraged.

Text footnotes should be numbered with Arabic numerals and inserted at the bottom of text. Footnote all personal communications, unpublished data, and unpublished manuscripts with full address of the communicator or author, or, as in the case of unpublished data, where the data are on file. Authors are advised to avoid references to nonstandard (gray) literature, such as internal, project, processed, or administrative reports. Where these references are used, please include whether they are available from NTIS (National Technical Information Service) or from some other public depository.

Literature cited comprises published works and those accepted for publication in peer reviewed literature (in press). Follow the name and year system for citation format. In the text, cite as follows: Smith and Jones (1977) or (Smith and Jones, 1977). If there is a sequence of citations, list alphabetically by author(s): Smith, 1987; Smith and Jones, 1985; Smith and Peterson, 1986. Abbreviations of serials should conform to abbreviations given in *Serial Sources for the BIOSIS Previews Database*. Authors are responsible for the accuracy and completeness of all citations.

Tables should not be excessive in size and must be cited in numerical order in the text. Headings within tables should be short but ample enough to allow the table to be intelligible on its own. All unusual symbols must be explained in the table legend. Other incidental comments may be footnoted with italic numerals. Use the asterisk only to indicate probability in statistical data. Zeros should precede all decimal points for values less than one.

Figures must be cited in numerical order in the text. The senior author's last name and the figure number should be written on the back of each one. Hand-drawn illustrations should be submitted as originals and not as photocopies. Submit photographs as glossy prints or slides with good contrast, otherwise we cannot guarantee a good final printed copy. Graphs should be submitted as laser-printed copies, not as photocopies. Label all figures with Helvetica typeface and capitalize the first letter of the first word in axis labels. Italicize species name and variables in equations. Use zeros before all decimal points. Use uppercase Times Roman bold typeface to label the parts of a figure, e.g. A, B, C, etc. Each figure legend should explain all symbols and abbreviations in the figure and should be double-spaced and placed at the end of the manuscript.

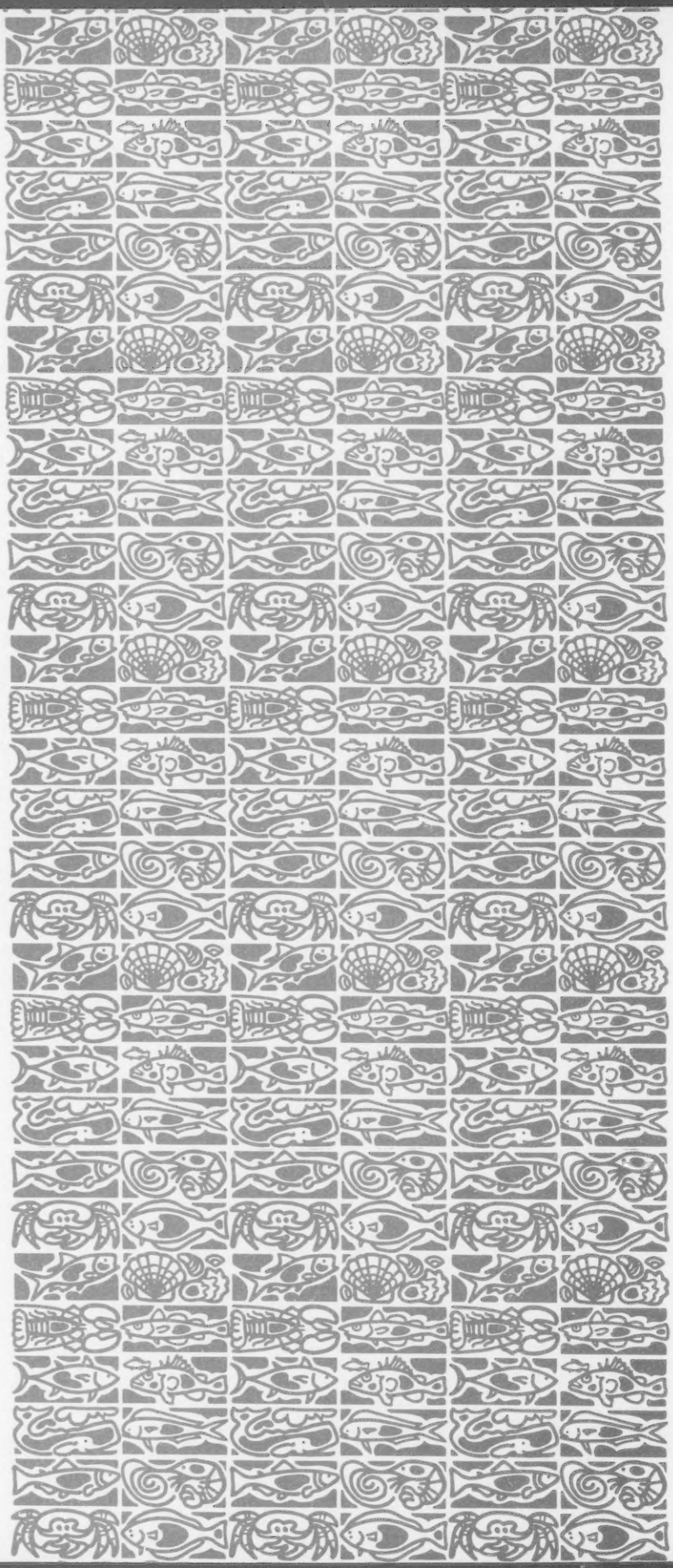
Copyright law Government publications are not copyrighted; they fall within the public domain. If an author reproduces any part of a government publication in his work, reference to source is appreciated.

Submission

Send printed copies (original and three copies without staples) to the Scientific Editor:

Dr. John V. Merriner
Southeast Fisheries Science Center
National Marine Fisheries Service
101 Pivers Island Road
Beaufort, NC 28516

Once the manuscript has been accepted for publication, you will be asked to submit an electronic copy of your manuscript to the Managing Editor. The electronic copy should be submitted in *WordPerfect* or *Microsoft Word* text format and placed on a 3.5-inch disk that is double-sided, double or high density, and that is compatible with either DOS or Macintosh systems.

A copy of page proofs will be sent to the author for final approval prior to publication.

Reprints (copies of published articles and notes) are available free of charge to the senior author (50 copies) and to his or her laboratory (50 copies). Additional copies may be purchased in lots of 100 when the author receives page proofs.